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Title:
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The impact of turbidity on the foraging ability and risk taking of two cichlid species: the invasive Nile tilapia (*Oreochromis niloticus*) and the threatened Manyara cichlid (*Oreochromis amphimelas*)

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A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of Master by Research in the Faculty of Life Sciences

School of Biological Sciences

Submission 10/2020

Word count: 13652

Abstract

Turbid waters are a natural part of productive aquatic habitats. However, turbidity does influence numerous fish behaviours, even when within the range of parameters found naturally. Human development is a major cause of increased turbidity and many agricultural, mining and building projects increase runoff into rivers and sedimentation. Turbidity restricts the visual ability of fish, changing the efficiency of foraging, reproduction and antipredator behaviour. How turbidity influences these reactions depends on the species and the life stage of the fish, further complicating the potential impact turbidity has on aquatic ecosystems. As the initial reaction to many types of environmental change is behavioural, studying how turbidity changes the behaviour of individuals will enable more accurate assessments of the impacts of environmental change on fish populations. To do this we tested the impact of turbidity on the Nile tilapia, *Oreochromis niloticus,* and the Manyara tilapia, *Oreochromis amphimelas.* The Nile tilapia is an invasive fish that increases turbidity in areas where the threatened Manyara tilapia resides, potentially contributing to the threatened status of the Manyara tilapia. We tested the impact of turbidity in two experiments that tested the foraging ability, antipredator behaviour and inter-individual consistent behaviours of both species across a range of turbidity. Our results suggest that rising turbidity increases the foraging efficiency of the Nile tilapia but the Manyara tilapia foraged most efficiently at the intermediate level of turbidity. In general, the Nile tilapia consumed more food than the Manyara tilapia. When no food was present, both species displayed increased antipredator behaviour in the higher turbidity as measured by increased shelter use. Neither species showed consistent inter-individual behaviour, i.e. personality, variation. Overall, the results indicate that turbidity is more advantageous for the Nile tilapia and so they are likely to outcompete the Manyara tilapia in turbid habitats.

Dedication and Acknowledgements

The author would like to thank C.I and T.C for their greatly appreciated help, guidance and support throughout the development and enaction of this study. He would also like to thank the whole Ioannou group and others at the University of Bristol for continued support and friendship throughout the process.

Author's declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's *Regulations and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

Part of this thesis has been submitted for peer review. Work in chapters two and three have been submitted for review in the journal Behavioral Ecology and Sociobiology and is posted as a preprint on BioRxiv under the title: The impact of turbidity on foraging and risk taking in the invasive Nile tilapia (Oreochromis niloticus) and a threatened native cichlid (Oreochromis amphimelas) (**doi:** https://doi.org/10.1101/2020.07.23.217513, authors: Jonathan D B Wing, Toby S Champneys, Christos C Ioannou). I, Jonathan D B Wing, led the writing on the paper and performed both experiments. I also conducted the statistical analysis with assistance from both Toby S Champneys and Christos C Ioannou.

SIGNED: J.D.B. Wing DATE: 10/2020

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Introduction

Human induced environmental change impacts animal behaviour in several ways, limiting the sensory information available, disrupting physiological processes, changing the structure of habitats and by introducing new species (Sih, et al., 2011; Tuomainen and Candolin, 2011). Human actions including mining, construction projects, boat traffic and deforestation increase the suspended sediment in water, increasing turbidity beyond natural limits (Hilton and Phillips, 1982; Brasington and Richards, 2000; Mol and Ouboter, 2004). Turbid water is filled with floating particles from sediment or algae that scatter the light traveling through it, creating cloudy water which is detrimental to the vision of fish (Davies-Colley and Smith, 2001). Intense farming practices increase the nutrients entering aquatic systems and accelerate algal growth, increasing turbidity (Bonnet et al., 2008). Turbidity is widely reported to alter a range of fish behaviours including feeding, reproduction and antipredator responses (Utne-Palm, 2002; Järvenpää, Diaz Pauli and Lindström, 2019; Sohel and Lindström, 2015). Despite this, turbid conditions are a natural feature of many aquatic habitats, and the transport of sediments into species rich areas such as estuaries maintain trophic food webs (Paudel et al., 2019). However, the impact of turbidity varies greatly between species and even those that reside in the same habitat can greatly vary in their level of tolerance to turbidity (Boubée et al., 1997).

A number of human developments alter light levels, artificially producing light or reducing the visibility within an area (Utne-Palm, 2002; Tuxbury and Salmon, 2005). The visibility of an object in water is dependent on the contrast between that object and its background (Utne-Palm, 2002). Turbidity scatters light and so distorts the images seen through water, this is detrimental to fish who have well developed eyes and rely primarily on vision for information concerning their surroundings (Guthrie and Muntz, 1986; Utne-Palm, 2002). Turbidity can provide shelter, restrict social interactions, change risk perception, limit sexual selection and can both help or hinder foraging (Hinshaw, 1985; Miner and Stein, 1996; Seehausen et al., 1997; Lehtiniemi, Engström-Öst and Viitasalo, 2005; Kimbell and

Morrell, 2015b; Lunt and Smee, 2015; Sohel and Lindström, 2015). Turbidity can also naturally fluctuate diurnally and seasonally, exposing species to a range of water clarities (Martin et al., 2019). The impact of reduced visibility on multiple behaviours makes studying the impact of unnatural turbidity important, to inform the management of ecosystems and ensure that appropriate actions are taken to prevent the decline of native species.

As turbidity disrupts the passage of light it could be assumed that its effect on behaviour are similar to the absence of light. Only a limited range of wavelengths can penetrate far into water, making the visibility of aquatic species at depth dependant on the intensity of light (Utne-Palm, 2002; Lythgoe, 1975). Studies have displayed differences in fish behaviour between species across a range of light intensities and combined with variations in turbidity. The lack a of universal response to turbid conditions is a result of the differences between the visual ability of fish species, which is significantly correlated with body size (Caves et al., 2017). Turbidity does not change the foraging efficiency of fish in darkness, demonstrating that turbidity can only influence vision when directly scattering the passage of light (Li et al., 2013). The intensity of light in water influences the impact that turbidity has on fish behaviour. High light levels can positively influence reaction distance in turbid conditions suggesting that light can offset the effects of turbidity (Utne, 1997). However, although high light intensity improves foraging, as it reduces so does foraging efficiency (Miner and Stein, 1996).

In comparison low light conditions with no turbidity are often more favourable for foraging than turbid water (Benfield and Minello, 1996). However, some species such as the largemouth bass, *Micropterus salmoides*, show a linear decline in foraging success as light levels reduce (McMahon and Holanov, 1995). These studies suggest that within some ranges, mainly at low intensities, light and turbidity independently have a similar effect on visually-reliant behaviour in fish.

The impact of turbidity on fish behaviour

Behavioural changes are one of the first measurable impacts that degraded habitats have on species (Wong and Candolin, 2015). The impact of turbidity on behaviour depends on the size, feeding strategy and species of fish. Smaller fish have a reduced field of vision in comparison to larger fish, reducing the number of particles that can potentially scatter light in their field of view (Utne-Palm, 2002). This allows juveniles to use the cover provided by turbidity to evade larger predators who find it comparatively harder to see while experiencing increased foraging efficiency (Gregory and Levings, 1996; Lehtiniemi et al., 2005). These differences in turbidity tolerance are also apparent between species in the same habitat. This has been observed in New Zealand freshwater habitats where the banded kokopu, *Galaxias fasciatus*, will try and avoid relatively low turbidity (17 NTU (Nephelometric turbidity units), whereas other fish who inhabit the same river system show the same avoidance at much higher levels (70 NTU for *Galaxias brevipinnis*, and 420 NTU for *Anguilla australis* and *Anguilla dieffenbachia*) or not at all (≤1100 NTU *Gobiomorphus huttoni*) (Boubée et al., 1997). This can also lead to differences in feeding behaviour between these species when in turbid conditions. Reduced feeding has been observed in the banded kokopu at levels as low as 20 NTU whereas *Gobiomorphus huttoni* display increased feeding rates as turbidity increases to 40 NTU which then decline as turbidity rises (Rowe & Dean, 1998). These variations between species has led to suggestions of catering water quality legislation to the requirements of the least tolerant species in the habitat (Boubée et al., 1997; Lloyd, 1987).

Reproduction

Many studies have highlighted the impact of turbidity on reproductive behaviour with turbidity influencing behaviour at multiple stages throughout the reproductive process. Sudden exposure to turbidity can force fish to move into open water, moving away from areas where reproduction occurs

and encouraging foraging behaviour instead (Gray et al., 2011). Although turbidity can force fish away from breeding areas the main effect of reduced vision on reproduction is through changing the interactions between mating pairs. Both Male and female fish take longer to inspect female partners in turbid water and the number of courtship behaviours expressed is reduced, lowering the likelihood of reproduction and limiting selection by restricting potential breeding interactions between males and females (Sundin, Berglund and Rosenqvist, 2010; Sebire et al., 2011; Engström-Öst and Candolin, 2007). However this can be beneficial for less productive individuals as turbidity can evenly distributes the possibility of any male fish reproducing, reducing the likelihood that a small number of males will monopolise reproduction with all the available females (Järvenpää, et al., 2019). Turbidity can also influence female behaviour and reduce the time invested in reproduction, resulting in females producing fewer eggs as they are unaware of competition from conspecifics (Järvenpää and Lindström, 2004). Water clarity can even influence the interactions between competing males, increasing courtship competition between them as turbidity increases aggressive behaviours (Gray et al., 2012).

Visual disruption can also directly influence the selection of colouration in multiple fish species. Male sticklebacks, *Gasterosteus aculeatus*, that stand out against their background are more likely to attract a female and reproduce, resulting in males with black colouration to be selected for in turbid conditions and red males to be selected for in clear water (Boughman, 2001; Lewandowski and Boughman, 2008). Similar observations have been made with the red shiner, *Cyprinella lutrensis*, which has more intense colouration in turbid environments (Dugas and Franssen, 2011). The selection of conspicuous spotted patterns has been observed in the green swordtail, *Xiphophorus helleri*, allowing easier conspecific detection in periods of seasonal turbidity (Franck et al., 2001). However, even if species have conspicuous coloration manipulating light conditions can alter the preference of females to displaying males (Seehausen and Van Alphen, 1998). This can result in closely related species which are only isolated by coloration reuniting. This has occurred in Lake Victoria habitats, where turbid water encourages dull colouration through predation, reducing species diversity as

distinguishing colour morphs sexually isolate closely related species (Seehausen et al., 1997). Similarly, reduced visual discrimination can also increase reproductive interactions between native and introduced species, potentially leading to hybridisation (Glotzbecker et al., 2015).

Foraging

Turbidity can reduce the foraging efficiency of many fish. This lack of tolerance is exhibited across a range of habitat types from coral reefs to clear water streams (Johansen and Jones, 2013; Becker et al., 2016). Low levels of turbidity (<10 NTU) are enough to decrease the rate of predators pursuing prey and significantly alter the probability of capture success in visually reliant predators (De Robertis et al., 2003; Johansen and Jones, 2013; Becker et al., 2016). The reactive distance of an individual, the maximum distance at which prey will be detected or pursued, is negatively affected as turbidity increases (Sweka and Hartman, 2003). This can restricts feeding success and reduces prey capture above 30 NTU (Harvey and White, 2008). However some species have a greater threshold of tolerance and experience a decline in capture success at levels exceeding 200 NTU (Huenemann et al., 2012). The avoidance of local turbid areas is often induced at low levels of sediment suspension, constraining individuals from areas that could potentially be rich in food (Johansen and Jones, 2013; Collin and Hart, 2015; Wenger et al., 2017). As the foraging of visually reliant species is often negatively affected by turbid conditions, olfactory reliant foragers are able to outcompete visual foragers in turbid environments (Lunt and Smee, 2015). However turbidity can improve foraging by providing nocturnal species with extended foraging periods (Hinshaw, 1985; Wenger et al., 2013a; Wishingrad et al., 2015; Li et al., 2013). Turbidity does not impair foraging of a number of species while they are juveniles, displaying that turbidity does not only provide cover, but also nutrition for developing juveniles (Wellington et al., 2010; Andree and Wahl, 2019).

Once foraging has begun in turbid water the chance that predator-prey encounters will occur is reduced, limiting consumption rates in ambush predators and potentially impacting growth rates and survival (Snow et al., 2018). This can reduce the likelihood of finding prey even in areas where prey are densely grouped (Turesson and Brönmark, 2007). Once a predator is close to prey, disrupted vision continues to hamper feeding success by lowering reactive distance, decreasing the detection radius of a predator and reducing the probability of it reacting to prey (Sweka and Hartman, 2003). Turbidity also influences the selectivity of prey, restricting a predator's choice, and can result in a single conspicuous species being focused on in turbid water (Shoup and Wahl, 2009). Food type also influences how turbidity influences fish, as visual piscivores require prey to stand out against a background for easy detection while planktivorous fish only need to find large swarms of prey to effectively forage (De Robertis et al., 2003).

Antipredator behaviour

Turbidity can provide cover for prey and leads to a predator becoming dependent upon encounter rates when foraging, negating the need for prey to perform antipredator behaviour and allowing more time to be allocated to food acquisition (Abrahams and Kattenfeld, 1997). This is beneficial to juveniles of a number of species, such as pike, *Esox lucius*, and perch, *Perca fluviatilis*, which decrease antipredator behaviour and reduce shelter use in turbid water (Lehtiniemi, Engström-Öst and Viitasalo, 2005; Snickars, Sandström and Mattila, 2004). Turbidity also allows fish to traverse their habitat easier, providing cover and reducing the chance of predation (Shingles et al., 2005; Ferrari et al., 2014; Gregory, 1993).

Despite turbidity often reducing antipredator behaviour, restricted vision can increase the perception of risk and encourage shelter use, reducing the time spent on other activities (Gauff et al., 2018). This can reduce the amount of risks an individual takes and result in more time being invested into decision

making to increase accuracy (Chamberlain and Ioannou, 2019). The mechanistic restriction of turbidity can also reduce the anti-predator response of individuals, as they can no longer see other group members to help inform antipredator actions (Kimbell and Morrell, 2015b). This results in the social cohesion of groups in turbid water to be reduced (Chamberlain and Ioannou, 2019). Intermediate levels of turbidity provide effective conditions for antipredator responses in a number of fish species, as individuals can take advantage of the increased contrast between a predator and their background and detect them earlier (Ehlman et al., 2019; Hinshaw, 1985). Species within the intermediate trophic level forage less in turbid water in the presence of top level predators, which benefits the survival of bottom level prey who are less likely to be predated upon (Figueiredo et al., 2016). This highlights the complex nature of predator prey interactions in turbid water that benefit some species while disadvantaging others

Rapidly changing environments threaten unadaptable species, increasing mortality and threatening their existence (Sih et al., 2011). If turbidity causes an individual to reduce antipredator behaviour when the level of threat does not change it may become more vulnerable to predation. Being unable to detect a predator reduces the likelihood of escape when an encounter event between predator and prey occurs. The development of predator recognition in fathead minnows, *Pimephales promelas*, is reduced in turbid water and hence restricts its ability to identify and escape potential predators (Chivers et al., 2013). The detection of predators by the fountain darter, *Etheostoma fonticola*, is impaired by turbid water even in the presence of olfactory cues, suggesting that visual cues are the most important sense for them to effectively avoid detection (Becker and Gabor, 2012). Escape success is reduced in turbid water for the juvenile cod, *Gadus morhua*, declining from 73% in clear water to 21% in turbid (Meager et al., 2006). Algal turbidity reduces the ability of sticklebacks to assess danger from avian predation, making them less likely to react to threats (Sohel and Lindström, 2015). The beneficial aspects of turbidity for predators are only apparent prior to prey encounters, as turbidity does not change capture success once prey has been detected (Becker et al., 2016). Even

though turbidity provides cover from visual predators, it does nothing to protect them from passive predators such as jellyfish (Ohata et al., 2011). This has been observed in juvenile red sea bream, *Pagrus major*, the ayu, *Plecoglossus altivelis* and in Japanese anchovy larvae, *Engraulis japonicus*, which suggests that the combination of turbidity and increasing populations of planktonic predators could be detrimental to the juvenile nurseys that are protected by turbidity (Ohata et al. 2011).

Visual disruption conceals the information transferred between conspecifics, limiting social interactions (van der Sluijs et al., 2011). This can restrict the formation of shoals, resulting in the creation of fragmented groups which will respond less effectively to threats (Kimbell and Morrell, 2015a). Aggregation is a common behaviour that is used in part to avoid predation, so breaking up groups will increase the likelihood of predation (Krause et al., 2002). This has been observed in a number of species including guppies, *Poecilia reticulata*, which are more likely to be alone in turbid conditions or will form smaller groups (Borner et al., 2015). Sticklebacks exposed to differently sized shoals in turbid water are just as likely to join either, but in clear water they spend more time closer to the larger shoal (Fischer and Frommen, 2013). Smaller shoals have weaker antipredator responses and turbidity encourages individuals to act independently, increasing the likelihood of freezing in response to threats (Kimbell and Morrell, 2015b). Despite this, turbidity can enhance schooling behaviour at moderate levels (Ohata et al., 2014).

Compensating for visual disruption

Sensory and behavioural changes can compensate for reduced vision in turbid water and increase the chance of finding food, conspecifics or detecting predators. In this section we will outline the mechanisms that allow fish to compensate for reduced vision in turbid environments.

The Lateral line

The lateral line is an sensory organ within fish running around the head and along the flanks of the body (Flock and Wersall, 1962). It consists of many hair like cells which respond to the movement of water and can be used to detect moving objects throughout the water column and on the water's surface (Bleckmann and Zelick, 2009). The reliance of fish on the lateral line system appears to vary between species according to the variance in the number of receptors they have, which has been recorded to be between 50 and into the thousands, indicating different reliance on water movement while navigating (Bleckmann and Zelick, 2009). However, a number of examples do show that some fish use this system to compensate for reduced visibility. Nocturnal predators such as the European catfish, *Silurus glanis*, depend on the lateral line system to follow the wakes made by prey in darkness and capture them (Pohlmann et al., 2004). Lateral line detection can also override vision in sunfish, *Lepomis cyanellus*, eliciting an automatic bite response when close to prey (Janssen and Corcoran, 1993). The use of the lateral line can also compensate for the prey detection of the peacock cichlid, *Aulonocara stuartgranti*, when in darkness, indicating the use of multiple senses when detecting prey (Schwalbe et al., 2012). The lateral line is also used to identify the presence of conspecifics and predators, and is used to initiate a rapid innate response to predation called the fast start, with the lateral line informing fish of potential danger and allowing it to evade a predators strike (Higham et al., 2015). Other antipredator behaviours such as schooling require acute sensitivity to the presence of other fish and studies have suggested that well developed lateral line organs provide a substantial advantage when schooling in turbid water (Ohata et al., 2014). Little research has been conducted on the lateral line's influence on compensating for turbid conditions but considering the role it can play in compensating for reduced vision in other contexts, species that depend heavily on the lateral line to detect objects may be at an advantage in turbid conditions compared to those with a reduced lateral line capability.

Olfaction

Chemoreception is an important sense for fish providing information that influence social, feeding, antipredator and reproductive behaviour (Hara, 1975). Chemoreception ability varies between fish, depending on the size of the olfactory organ and the amount of water that is able to flow over it (Hara, 1975). Olfactory cues inform fish on the presence of an object in a large area that may not be directly visible, whereas a visual stimulus provides immediate information of an object exposed to light (Hartman and Abrahams, 2000; Chivers et al., 2001). Olfactory cues increase the foraging motivation of visually reliant fish in turbid water even though limited vision restricts the ability to detect food (Johannesen et al., 2012). Guppies compensate for low light conditions by switching from visual to olfactory cues, increasing the chance of foraging success (Chapman et al., 2010). Juvenile cod use both chemosensory and visual cues when foraging in turbid water to increase the likelihood of finding food (Meager et al., 2005). This also can be seen in sticklebacks, whose foraging is affected by turbidity only when combined with highly saturated olfactory cues, suggesting olfaction is used to compensate for turbid conditions (Quesenberry et al., 2007; Webster et al., 2007).

Olfactory and visual cues provide different antipredator responses, so the visually constrictive nature of turbidity may change predator-prey interactions. Olfactory and visual predator cues inform prey on when it is safe to move between open water and sheltered areas, so restricting vision can result in prey being vulnerable in the presence of predators (Martin et al., 2010). To compensate, fish use olfactory cues to inform antipredator behaviour in turbid water and thus reduce the chance of a predator finding them (Leahy et al., 2011). This can even enhance the detection of predators, observed in mosquitofish, *Gambusia holbrooki*, that express increased and repeatable antipredator behaviour in medium levels of turbidity combined with predator cues (Ehlman et al., 2019). However, If prolonged exposure to turbidity occurs fish will rely more heavily on olfactory cues than visual stimulus (Suriyampola, Cacéres and Martins, 2018). Prey can further increase the efficiency of predator

recognition by learning the olfactory cues of specific predators and improving their antipredator behaviour (Utne-Palm, 2001). This recognition is further displayed in the interactions between conspecifics. The use of olfactory cues in the recognition of stickleback conspecifics is much higher in populations who are exposed to turbid environments than individuals in clear water (Hiermes et al., 2015). Conspecific alarm cues can elicit similar responses compared to visual cues from a predator, showing how conspecifics can improve the chance of evading predation in turbid water (McCormick and Manassa, 2008).

Behavioural compensation

Behavioural changes can also help fish compensate for reduced vision. Zebrafish, *Danio rerio,* with experience of turbid water respond less effectively to visual cues than olfactory ones, shifting to olfactory cues for their primary sense during navigation (Suriyampola et al., 2018). Populations of guppies reared in turbid water have a greater response to olfactory cues, increasing foraging efficiency in low light habitats, but this low light adaption reduces the ability to detect visual cues (Chapman et al., 2010). This suggests that populations reared in long term turbid environments could potentially be at a disadvantage if a sudden increase in water clarity makes the environment more suited to visual foraging.

The longer prey have to detect a predator, the more time that prey has to react and escape, and in response, predators increase activity and attack speed to increase the chance of successfully capturing prey (Lima and Dill, 1990; Werner and Anholt, 1993; Sweka and Hartman, 2001; Granqvist and Mattila, 2004; Meager et al., 2006; Harvey and White, 2008). This compensatory mechanism used by fish in turbid water explains the lack of change in foraging efficiency between different levels of turbidity (Figueiredo et al., 2016). Although these behaviours may increase foraging efficiency, energy

expenditure is higher and lower growth rates are observed in turbid conditions (Sweka and Hartman, 2001).

Using landmarks when navigating in turbid water reduces feeding latency, indicating that spatial learning can improve foraging success (Sekhar et al., 2019). The use of landmarks as a reliable indicator of location is more prevalent in stable environments, for example, ponds and lakes (Odling-Smee and Braithwaite, 2003). This indicates that the negative effects of turbidity may be reduced in these stable environments, as navigational aids such as landmarks improve foraging success. To ensure conspecifics can communicate in turbid water, exaggerated forms of communication are used, as seen in brown trout, *Salmo trutta*, who amplify visual displays to reduce the aggression of dominant individuals in turbid water (Eaton and Sloman, 2011). Fish that have previously been exposed to turbid conditions show no change of social behaviour in turbid water, suggesting that a combination of sensory mechanisms are used in social interactions (Suriyampola et al., 2018). These adaptations allow fish to compensate for the disadvantages of reduced vision but will ultimately be at the expense of other important behaviours such as reproduction or predator avoidance, reducing their efficiency (Sweka and Hartman, 2001; Webster et al., 2007).

Wider impacts of turbidity and habitat degradation

Apart from the direct behavioural impacts associated with turbid water, increased sedimentation negatively impacts aquatic communities in a number of other ways. Reduced light penetration restricts the growth of primary producers and limits food sources for higher tropic levels (Henley et al., 2000). This can occur at relatively low levels of turbidity reducing primary production by up to 50% at 25 NTU (Lloyd et al., 1987). Sedimentation also removes habitats for macroinvertebrates and limits oxygen levels reducing invertebrate abundance by up to a 40% (Ryan, 1991). Increases in turbidity resulting from dredging contribute to the loss of seagrass beds, an important habitat that prevents

costal erosion and is vital to fisheries (Erftemeijer and Robin Lewis, 2006). A number of coral species are also venerable from costal dredging due to increases in turbidity (Erftemeijer et al., 2012). The combined impact of high levels of turbidity restricting foraging efficiency through reduced vision and reducing the abundance of available food sources and available habitats are likely to further negatively impact the populations of fish species in turbid environments.

High levels of suspended solids can irritate the gills of fish and reduce respiratory efficiency, which reduces growth rates, increases stress and reduces the fitness of fish (Horkel and Pearson, 1976; Henley et al., 2000; Sutherland and Meyer, 2007). Sedimentation reduces the size of potential spawning areas and smothers eggs, depriving them of oxygen and reducing reproductive success (Henley et al., 2000). The combination of these and the behavioural impacts of turbidity leads to changes in community composition in areas of long term chronic turbidity, allowing species that do not rely on visual cues and are tolerant of suspended solids to dominate (Lunt and Smee, 2014, 2015). The diversity of species is reduced in degraded habitats and they become vulnerable to colonisation by invasive species (Linde et al., 2008). A number of species are successful because of their tolerance of degraded habitats, being able to thrive in areas where native specialist species are declining (Linde-Arias et al., 2008; MacDougall and Turkington, 2005). As avoidance of turbid habitats can be induced by as little as 15 NTU, the potential of prolonged sedimentation encouraging the dominance of invasive species is likely (Boubée et al., 1997). Some invasive species also increase turbidity as part of natural foraging behaviour, increasing nutrients and suspended particles in the water column (Zambrano and Hinojosa, 1999; Zhang, Mei and Gulati, 2017).

Conclusion

The impact of turbidity on fish is context dependant and relies on the tolerance of each species**.** This makes investigating the impacts of turbidity important as numerous outcomes could occur when

human activity results in reduced water clarity. As turbidity can both positively and negatively influence fish behaviour, comparing the responses of species who are likely to interact is important to gain the greatest understanding of the effects on natural ecosystems. We carried out two experiments that assessed the impact of turbidity on two species of fish, the Nile tilapia, *Oreochromis niloticus*, and *Oreochromis amphimelas*. *O. amphimelas* is native to Tanzania and is likely to be sharing habitats with *O. niloticus* due to anthropogenic introductions (Shechonge et al. 2019). *O. niloticus* increases turbidity during foraging and is well known to reside in degraded turbid habitats (Linde et al. 2008; Zhang et al. 2017). We aimed to assess how turbidity impacts the behaviour of *O. niloticus* and *O. amphimelas* in similar ways. This was done by testing the efficiency of foraging, antipredator behaviour, and the inter-individual consistent variation of both species. Considering the tolerance of *O. niloticus* to turbid environments (Linde et al., 2008). We predicted that *O. niloticus* will feed more efficiently and not change its antipredator behaviour in turbid water, indicating an ability to potentially outcompete the native *O. amphimelas.*

The effect of turbidity on the foraging efficiency of the invasive Nile tilapia, *Oreochromis niloticus*, and the Manyara tilapia *Oreochromis amphimelas*

Abstract

We investigated the effect of turbidity on the foraging ability of the invasive Nile tilapia *Oreochromis niloticus* and the threatened Manyara tilapia *Oreochromis amphimelas*. Under standardised laboratory conditions we recorded the time taken to initiate feeding, the total number of food items that were attempted to be consumed (feed attempts) and the total number of food items consumed in three levels of turbidity (0,15 and 30 NTU). Turbidity had no impact on the latency of *O. amphimelas* to forage but *O. niloticus* initiated foraging earlier in turbid water. The number of feed attempts by *O. niloticus* increased as turbidity increased but in *O. amphimelas*, the number of feed attempts was greatest in the intermediate turbidity. *O. niloticus* consumed more items with no significance effect of turbidity in either species. These results indicate that turbidity is beneficial for *O. niloticus* foraging and improves *O. amphimelas* foraging at intermediate levels. We explain these results with potential compensatory behaviours used in turbid environments, visual benefits of intermediate levels of turbidity and the antipredator benefits of turbid conditions. Our findings show that the presence of turbidity is more beneficial to the foraging of *O. niloticus* than *O. amphimelas*, which further reinforces the potential threat that *O. niloticus* poses to competitors in natural habitats.

Keywords: habitat degradation, environmental stressors, invasive species, visual acuity, feeding latency, sensory compensation.

Introduction

Particles suspended in water scatter light as it travels through it, creating cloudy water that alters the contrast of an objects and its background (Utne-Palm, 2002). Turbidity limits the visual information available, negatively impacting the foraging success of visually reliant species (Pekcan-Hekim and Lappalainen, 2006; Lunt and Smee, 2015). Reducing foraging efficiency lowers growth rates which negatively impact populations (Huenemann, Dibble and Fleming, 2012; Becker et al., 2016). Despite this, low levels of turbidity can alter the contrast of food items against their background and make them easier to detect (Martin et al., 2019; Hinshaw, 1985). Therefore, investigating the point at which turbidity starts to negatively impact foraging is important as a lack of behavioural plasticity in response to environmental change will negatively impact biodiversity (Tuomainen and Candolin, 2011).

The foraging success of visual foragers is negatively impacted by turbid water. This is due to turbidity's negative effects on prey detection, reducing the reaction distance of predators (Barrett et al*.,* 1992; Gregory, 1993; Sweka and Hartman, 2003; Quesenberry et al*.,* 2007). This results in turbidity increasing the latency to forage and reducing foraging efficiency (Becker et al., 2016). This has been observed numerous times, for example largemouth bass, *Micropterus salmoides,* turbid conditions increase the time taken to locate and interact with potential food, influencing individual fitness (Huenemann et al., 2012). Turbid environments reduce the foraging efficiency of smallmouth bass, *Micropterus dolomieu*, more than the presence of sheltered areas for prey which influences selectivity (Carter et al., 2010). Planktonic damselfish, *Pomacentridae*, also see reductions in attack success by up to 69% in low levels of turbidity (8 NTU) (Johansen and Jones, 2013).

Increased turbidity can lead to planktivorous reef fish to develop a preference for immobile prey when foraging as they are easier to obtain in turbid conditions. (Johansen and Jones, 2013). Reduced visibility prompts foragers to stop differentiating between prey and instead feed whenever an

opportunity presents itself, gaining the maximum available energy from limited encounter situations (Kimbell and Morrell, 2016; Snow et al., 2018). This is in response to turbidity reducing the reactive distance of fish and allowing prey to escape easier in turbid water, reducing the chance of successful capture (De Robertis et al., 2003). Turbidity also influences where a fish swims in the water column while foraging. In moderate turbidity fish will have a greater feeding success when foraging benthically than higher up in the water column (Harvey and White, 2008).

Fish in turbid waters may have a reduced foraging efficiency compared to those in clear waters but can compensate by changing feeding strategies (Hecht and van der Lingen, 1992). Several behaviours have been observed that offset the negative effects of turbidity. Increasing activity compensates for reduced reaction distance in turbid water, increasing the likelihood of finding prey by increasing encounter rates (Sweka and Hartman, 2001; Granqvist and Mattila, 2004; Harvey and White, 2008). This is seen in pike who increase activity in turbid conditions (Andersen et al., 2008). Rainbow trout, *Onochorynchus mykiss*, also increase movement and switch to active prey searching from drift feeding in turbid water, increasing the number of prey captured (Sweka and Hartman, 2001). Although this compensatory behaviour is potentially detrimental if the time taken to find prey is not reduced while energetic costs increase (Meager and Batty, 2007). However some species do not need to compensate as they have a high level of tolerance to the visual disruption caused by turbidity (Stuart-Smith et al., 2007).

The introduction of invasive species can have a direct negative effect on the abundance of native fish species within a habitat (Gallardo et al., 2016). If an invasive species is tolerant of highly turbid conditions the decline of a habitat allows them to outcompete and reduce the presence of native species (Linde et al., 2008). As well as adapting to already degraded habitats some invasive species increase turbidity, for example carp, *Cyprinus carpio*, and *O. niloticus* who disturb sediment while foraging and increase nutrient loading (Zambrano and Hinojosa, 1999; Linde-Arias et al., 2008). The

combination of changes in water clarity and the presence of invasive species can further disadvantage native species. The presence of turbidity increases the dominance of the invasive yellowfin shiner, *Notropis lutipinnis*, over the royside dace, *Clinostomus funduloides*, resulting in it being able to acquire better foraging positions and outcompeting native species (Hazelton and Grossman, 2009). As dominant fish are more than three times as likely to capture prey than other fish in both of these species, the presence of turbidity will impact the royside dace both through competition and by reducing their reaction distance (Hazelton and Grossman, 2009a). The combinations of degraded habitats and invasive species can negatively impact native biodiversity, as species are unable to adapt to both threats simultaneously (Mainka and Howard, 2010).

We will investigate the impacts of turbidity on the foraging efficiency of the *Oreochromis niloticus,* and the *Oreochromis amphimelas*. *O. niloticus* has established numerous invasive populations across the tropics, from south America to Africa, as a result of its popularity in aquaculture and subsequent releases into the wild (Shechonge et al., 2019, Zengeya et al., 2013). *O. amphimelas* is a threatened species native to Lake Manyara and other lakes in Tanzania (Shechonge et al., 2019). Little is known of its foraging behaviour or its behavioural flexibility in changing environments. *O. niloticus* has a wide invasive presence in Africa and studies suggests that populations are likely to appear in areas where exotic species have yet to be introduced (Zengeya et al., 2013). The presence of *O. niloticus* is also threatening to native *Oreochromis* species as hybridisation is thought to be likely (Shechonge et al., 2019). We aimed to investigate how the foraging of both species is impacted by turbidity and if differences in foraging performance are likely to influence the competition between them. We predicted that increased turbidity will have a detrimental effect on the foraging ability of *O. amphimelas* and a positive or neutral effect on the foraging of *O. niloticus.*

Method

Subjects

O. amphimelas were supplied by Bangor University in December 2018 and *O. niloticus* subjects were purchased from Fish Farm UK London in December 2018. The *O. amphimelas* were 2nd generation captive bred fish reared from ancestors collected in the wild. Both species were housed in clear water before moving to Bristol university. 36 *O. amphimelas* (65.3 ± 7.5 mm mean ± S.D body length) and 36 *O. niloticus* (79.6 ± 6.9 mm mean ± S.D total body length) were housed in 180-litre glass tanks in clear water within a recirculating aquarium system. Enrichment was provided for the fish by placing plastic pipes and plants in the housing tanks (Brydges and Braithwaite, 2009). Fish were fed flake and granular food, blood worm or vegetarian frozen food once per day. Water temperature was kept at 26°C and the room was lit with a consistent diurnal cycle of 12:12 hours (light: dark).

Experimental setup

Trials took place in a white acrylic tank separated with an opaque divider to create two areas (each 80.5 cm x 64 cm x 15 cm (length x width x height) Fig. 1) allowing two trials to occur at the same time. In each trial one *O. amphimelas* was tested on one side of the tank, and one *O. niloticus* on the other side. The tank was filled to a depth of 15cm with aged water (77.2 litres). This water depth was used to allow practical observation and recording of the experiment with a similar depth being used in other experiments of fish in turbid water (Rowe & Dean, 1998; Kimbell & Morrell, 2016). The tank was lit and recorded from above with a Gopro Hero 5 Black at a resolution of 1920 x 1080 pixels. A white curtain was drawn across the side of the tank separating it from the rest of the room to avoid disturbances. Trials were conducted between the 30.04.2019 and 14.05.2019.

Procedure

Each day, a randomly selected level of turbidity (0, 15 and 30 NTU) was created and 12 individuals (6 of each species) were tested at this turbidity. Turbidity was created using kaolin clay by adding 0.04 mg/l for 15 NTU and 0.09 mg/l for 30 NTU. Following previous studies the kaolin clay was sprinkled evenly across both sections of the tank and mixed until the desired turbidity was attained (Quesenberry, et al*,*. 2007; Leahy et al*.*, 2011). The levels of turbidity used in the study were below the upper tolerance for other species previously tested and were not high enough to interfere with the detection of chemical cues or change the pH and hardness of the water (Horppila et al*.,* 2004; Leahy et al*.*, 2011). The keen olfactory ability of tilapia and the suitability of *O. niloticus* to degraded turbid habitats suggests this upper tolerance also applies to our subject species (Linde et al., 2008; Marusov and Kasumyan, 2017). A common consequence of anthropomorphic activities such as mining, is to increase the amount clay entering an aquatic systems, this makes clay an ecologically relevant way of testing the effects of increased turbidity on fish (Kemp et al., 2011; Eriksson et al., 2004). To ensure that the turbidity level kept constant across all trials, stirring was conducted between each trial, resuspending clay and then measured to ensure a consistent turbidity level was maintained throughout the trials.

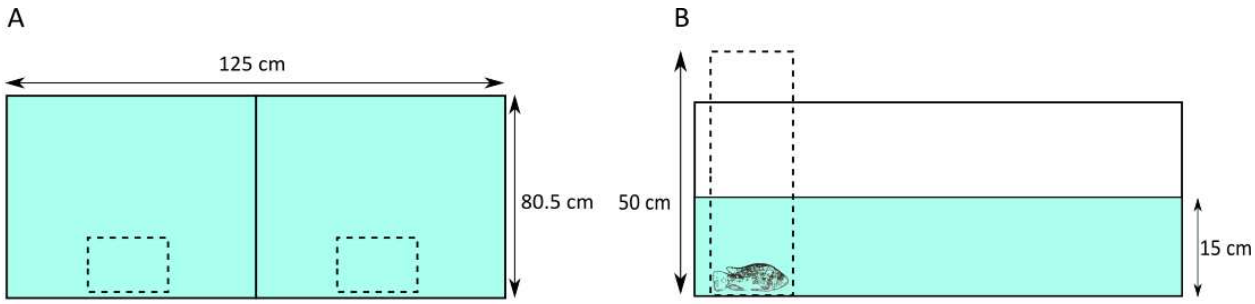

Figure 1. Experimental arena used to determine the effects of turbidity on the foraging efficiency of *O. niloticus* and *O. amphimelas*. Displaying (A) a top-down view of the experimental arena and the position of the acclimation boxes within each side (dashed) and (B) a cross-section of the trial arena, with the removable acclimation box (dashed).

The day before each trial, a hand net was used to haphazardly catch 6 fish of each species from the stock tanks. These fish were acclimatised to the next day's turbidity (0, 15 or 30 NTU) for 16 hours (overnight) in the trial tank prior to testing. The fish were separated by species in both sides of the tank. The fish were not fed across the acclimatising period to encourage feeding and standardise motivation. Prior to the first trial of the day, all participants were removed from the experimental arena and stored in covered plastic containers (45 x 32 x 25 cm, length, width, height, (water depth 15cm, water volume 21.6 litres)). These containers were placed in water that matched the days treatment and fish were separated by species. 30 minutes before the start of a trial an *O. niloticus* and an *O. amphimelas* were netted and measured (mouth to the end of caudal fin) with digital callipers. They were then placed in an acclimation box in the trial area for 30 minutes before trials began (Fig. 1B). After the acclimation period had passed 10 food pellets were spread evenly across each side of the experimental arena opposite the fish in the acclimation boxes. The pellets used in the experiment floated at the water's surface to ensure that every feed attempt could be easily seen in turbid conditions (Hikari Cichlid Gold mini-pellet, 3.2-3.7mm). The camera was then turned on and the acclimation boxes were slowly removed, releasing the fish. Each fish only took part in the trial once and were then place into a regular housing tank reserved for individuals who had already completed

the trial to ensure they did not participate more than once. Each trial lasted 15 minutes and at the end of the days trials the tank water was emptied and replaced with fresh aged water. This was then dosed with the desired turbidity for the next day. The next group of fish was then acclimated for the next day's trial.

To ensure the consistent recording of results a single reviewer analysed all video recordings. BORIS software version 7.7.3 was used for all analysis (Friard and Gamba, 2016). For each trial the latency to first feed, the number of feeding attempts (the number of the 10 pellets that the fish attempted to feed on) and the number of pellets consumed were recorded. If a fish did not attempt to feed, a maximum score of 900 seconds was awarded to that individual. A feeding attempt was defined as an individual attempting to feed on a single pellet only once, and all subsequent attempts to feed on that pellet were not counted. This was to ensure that the measurements recorded were of fish discovering novel food items. All procedures were approved by the University of Bristol Ethical Review Group, UIN UB 18 067.

Statistical analysis

R version 3.5.3 was used for all analysis (R Core Team, 2019). Latency to first feed, a censored time-to-event response variable, was analysed with a Cox proportional hazard test. The covariates were the level of turbidity, total body length and species. This requires the assumption that the hazards are proportional and the covariates don't change over time. If this is not the case, a more complex version of the analysis is required where the trial period is divided (Hess, 1995). This was tested for using the Schoenfeld residuals (R function "cox.zph", in the "survival" package) (Therneau, 2015). The Martingale residuals were used to test the assumption of non-linearity (R function "ggcoxfunctional", in the "survminer" package) and the deviance residuals were used to examine influential observations

(R function “ggcoxdiagnostics”, in the “survminer” package) (Kassambara, Kosinski and Biecek, 2019). As these assumptions were hence met, non-adjusted survival analysis was used to test the latency to first feed as a function of turbidity treatment, species and body length across the 900 second trials.

The number of feed attempts was analysed with negative binomial GLMs (generalised linear models). To make sure either model was not overdispersed the continuous variables were scaled (R function “scale”), then the dispersion parameters were calculated to confirm they were between 0.5 and 2 (Duffield and Ioannou, 2017). The number of feed attempts model included an interaction term between species and turbidity and their main effects, a continuous variable (body length) and a categorical variable (side of arena). After observing a nonlinear relationship between turbidity and the response variables polynomial regression was applied to provide a nonlinear fit to the model for the number the models (R function “poly”) (Becker et al*.,* 1989; James et al*.*, 2000; Chambers and Hastie, 2017). Nonsignificant interactions or explanatory variables were then removed by deleting terms based on likelihood ratio tests (using R function “drop1” in the lme4 package) (Mazerolle, 2017).

The number of pellets consumed was also analysed with negative binomial GLMs. The model initially included an interaction term between species and turbidity and their main effects, including continuous (body length) and categorical (side of arena) predictor variables. Further negative binomial GLM models were created for each species individually to investigate the main effect of turbidity including continuous (body length) and categorical (side of arena) predictor variables. To reduce overdispersion, the continuous variables were scaled on both models (R function “scale”). Nonsignificant interactions or explanatory variables were then removed by deleting terms based on likelihood ratio tests (using R function “drop1” in the lme4 package) (Mazerolle, 2017).

Results

The likelihood *O. amphimelas* performing the 1st feed attempt was significantly lower than *O. niloticus* across all treatments (Cox Proportional hazard model (CPH): hazard ratio (HZ) = 0.21, N = 72, $P < 0.001$; Fig. 2). Turbidity did not affect the likelihood of the first feeding attempt in *O. amphimelas* (0 NTU versus 15 NTU CPH: HZ = 0.8, N = 36, $P = 0.64$; 0 NTU versus 30 NTU, CPH: HZ = 0.58, N = 36, $P = 0.29$; 15 NTU versus 30 NTU CPH: HZ = 0.72, N = 36, $P = 0.53$; Fig. 2A). *O. niloticus* was more likely to feed at 15 and 30 NTU than at 0 NTU (0 NTU versus 15 NTU CPH: HZ = 2.5, N = 36, $P = 0.04$; 0 NTU versus 30 NTU CPH: HZ = 2.29, N = 36, $P = 0.005$; Fig. 2B). Turbidity had no effect on feeding likelihood between 15 NTU versus 30 NTU (CPH: HZ = 0.91, N = 36, $P = 0.83$).

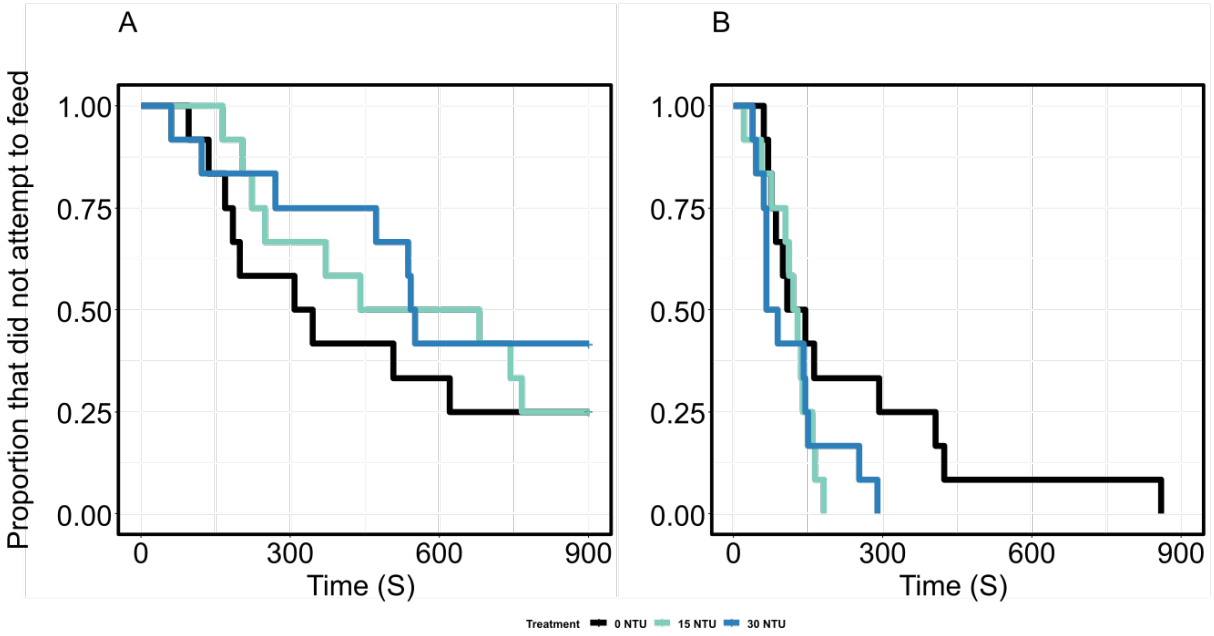

Figure 2. Kaplan-Meier estimates of latency to the first feeding attempt proportion by (A) *O. amphimelas* and (B) *O. niloticus* for each treatment levels of turbidity.

When the model was restricted to fitting a linear relationship between turbidity and the number of the food items that were discovered and the fish attempted to feed on (i.e. feed attempts), there was no significant interaction between species and turbidity (negative binomial GLM: species *

(scale(turbidity)): $LRT_{1,66}$ = 0.02, *P* = 0.88) or a linear effect on turbidity (negative binomial GLM: (scale(turbidity)): $LRT_{1,67}$ = 1.18, *P* = 0.27). The effect of species was significant and *O. niloticus* attempted to feed on a greater number of food items than *O. amphimelas* (negative binomial GLM: species: $LRT_{1,67}$ = 63.77, *P* = < 0.001). Adding a quadratic term for turbidity, however, resulted in a significant interaction between turbidity and species (negative binomial GLM: species * poly(scale(turbidity)): $LRT_{2,64}$ = 11.1, *P* = 0.003). This interaction and the trends in Fig. 3a suggest that the number of feed attempts by *O. amphimelas* was the greatest at the intermediate turbidity, but there was no such quadratic relationship in the trials with *O. niloticus*.

No effect on pellet consumption was found in the interaction of species and turbidity (negative binomial GLM: species * (scale(turbidity)): $LRT_{1,66}$ = 1.19, *P* = 0.27; Fig. 3B). As main effects, turbidity did not affect how many pellets were consumed (negative binomial GLM: (scale(turbidity)): $LRT_{1,67}$ = 3.29, *P* = 0.06) but *O. amphimelas* consumed less than *O. niloticus* (negative binomial GLM: species: $LRT_{1,66}$ = 13.87, *P* < 0.001). Analysing the data separately by species displayed that turbidity did not affect the number of pellets consumed by *O. amphimelas* (negative binomial GLM: (scale(turbidity)): $LRT_{1,32}$ = 0.76, *P* = 0.38) or *O. niloticus* (negative binomial GLM: (scale(turbidity)): $LRT_{1,32}$ = 1.36, *P* = 0.24).

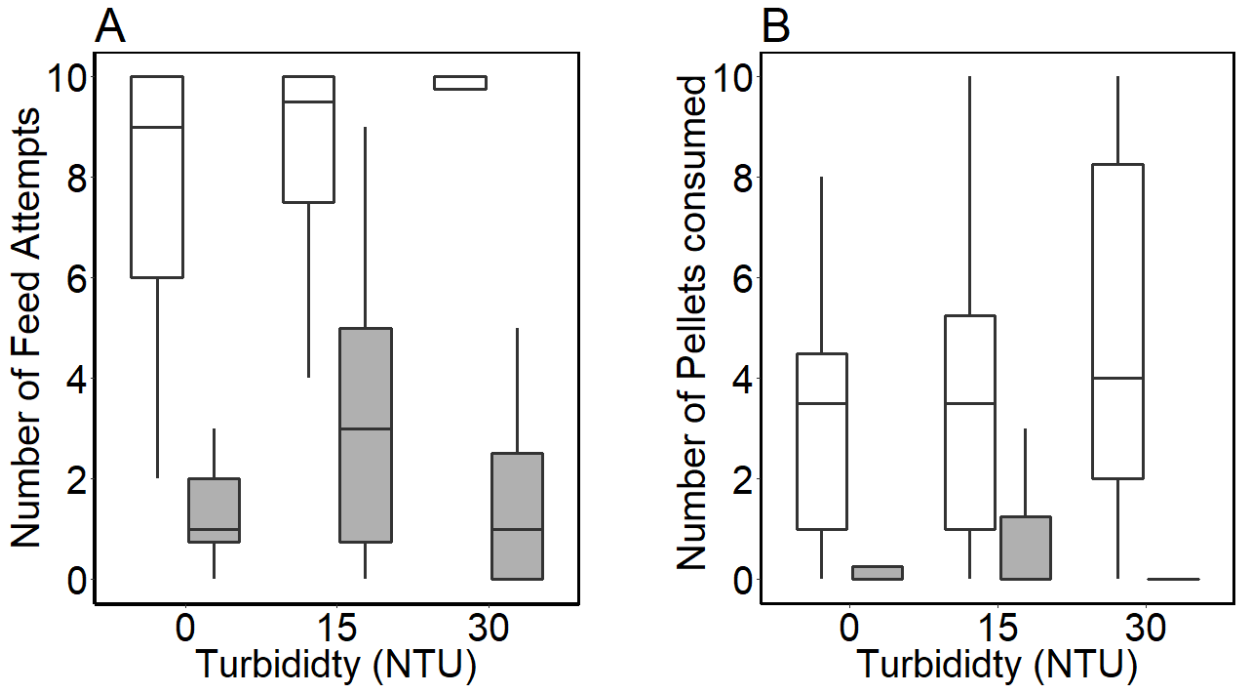

Figure 3. (A) The number of feed attempts and (B) pellets consumed across treatments for both species, *O. niloticus* (white) and *O. amphimelas* (grey). The boxes represent the interquartile range with the middle line displaying the median. Each whisker represents the position of 50% of values outside of the interquartile range.

Discussion

We predicted that the presence of turbidity would impact the foraging of *O. amphimelas* negatively and the foraging of *O. niloticus* positively or neutrally. The results indicate that *O. niloticus* was more likely to attempt to feed sooner in turbid water than *O. amphimelas. O. amphimelas* saw no change in feeding likelihood between treatments. The feed attempts of *O. niloticus* increased as turbidity increased but *O. amphimelas* showed the greatest number of feed attempts at the intermediate level of turbidity. The number of pellets consumed by either species was not influenced by turbidity but *O. niloticus* consumed more across treatments. Overall, our results demonstrate that the foraging ability of *O. niloticus* increases in turbid water, and rises as turbidity rises. Although some improvement to object detection is seen in *O. amphimelas* at 15 NTU overall foraging performance is not significantly influenced by turbidity. Our results are typical of the literature covering the effects of turbidity on foraging, showing how differently two species react when exposed to similar sensory conditions. Therefore, the combination of *O. niloticus* and turbidity levels above 15 NTU may constrict the foraging of *O. amphimelas* both through intraspecific competition and reduced object detection. This is especially relevant considering the current geographic range of *O. niloticus* which is now thought to overlap with that of *O. amphimelas* (Shechonge et al., 2019).

Turbidity can influence the foraging behaviour of aquatic species in a positive, negative and non-linear way depending on its intensity (Hinshaw, 1985; Meager et al., 2005; Pekcan-Hekim and Lappalainen, 2006). Low levels of turbidity can have a negative impact on foraging and reducing foraging latency, reaction distance and attack success (Gregory and Levings, 1996; Miner and Stein, 1996; Becker et al., 2016). This is not consistent with our results which show turbid water impacting foraging positively or neutrally. This indicates that foraging is not constrained by turbidity in either species, or they are able to compensate for disrupted vision by utilizing other senses and behaviours. Olfactory cues are often used together with vision, and fish that have been exposed to turbidity for extended periods

(days/months/years) change to olfactory from visual cues to forage (Chapman et al., 2010). This is despite the fact that olfactory cues are slow moving and do not provide reliable information on the exact whereabouts of an object, instead increasing individual motivation to search for food in the immediate area of the cues location (Johannesen et al., 2012). This could explain the lack of negative impact of turbidity on foraging of both as species were acclimatised overnight in turbid water before the trial. This could suggest that short term sudden discharges of sedimentation may have more negative impact than chronic exposure that allows fish time to adjust. Therefore, limiting widespread introductions of turbidity inducing fish such as *O. niloticus* will limit its change on the environment and potential impact on native species.

O. niloticus is an adept forager and has been observed successfully foraging using only olfaction and the sense of touch, indicating that it does not require vision to forage (Marusov and Kasumyan, 2017). This could explain the increase in likelihood of *O. niloticus* to first forage in turbid water, as olfactory dependent species are not affected when foraging in turbid waters (Lunt and Smee, 2015). However, this does not explain the variation in the likelihood to first forage between turbid and clear treatments. If *O. niloticus* was reliant only on olfaction for foraging the presence of turbidity would not change its foraging latency. Instead, it appears that *O. niloticus* depends on its sense of olfaction to detect the presence of food within an area, triggering the motivation to forage and prompting an increase in activity which goes on to increase the likelihood of encounter events. A common response that improves foraging efficiency when visibility is reduced is to increase activity, raising the probability of encounter events (Sweka and Hartman, 2001; Granqvist and Mattila, 2004; Harvey and White, 2008). Similar studies have acknowledged the importance of initial detection while foraging showing that turbid waters reduce reactive distance when foraging but not foraging success once food is detected (Sweka and Hartman, 2001; Quesenberry et al., 2007). This implies that greater activity results in higher foraging success, although this may only be beneficial in our relatively small trial area.

The lack of change in the likelihood of *O. amphimelas* to first feed suggests a similar compensatory mechanism is used to negate the effect of turbidity on its first feed attempt. However, the additions of the quadratic term to the feed attempt model indicates that O. *amphimelas* has a hump-shaped relationship between turbidity and feed attempts, being greatest at the intermediate level of turbidity. This indicates that for *O. amphimelas*, objection detection is most effective in the intermediate treatment. Moderate levels of turbidity can be beneficial to foraging, lowering a foragers perception of predation and being visually beneficial (Pangle et al., 2012; Gregory, 1993; De Robertis et al., 2003; Hinshaw, 1985). This is attributed to the change in contrast that allows objects to stand out in turbid water (Hinshaw, 1985). This suggest that for *O. amphimelas*, 15 NTU is visually advantageous when foraging but does not increase the motivation to initially begin foraging.

Despite turbidity influencing the feed attempts of both species' consumption was unaffected. This is in contrast to previous studies that suggest that turbidity only influences the initial detection of an object rather than capture success (Sweka and Hartman, 2003; Quesenberry et al., 2007). Several pellets were frequently spat out by individuals during the trials, possibly indicating that the food source was difficult to handle and reorientation was needed (Croy and Hughes, 1991). Additionally, the food source used in the experiment was not routinely fed to the fish and was used for the practical reason of keeping the fish in view to allow it to be seen by the camera in turbid water. This could indicate that the reason that *O. amphimelas* was outcompeted by *O. niloticus* is due to it being less likely to enter novel situations and being less bold than *O. niloticus.* Future studies may consider using different food sources that are both visible for recording and easy to consume, or enacting trials that have a food source that is free floating within the water column (Chamberlain and Ioannou, 2019, Mauzè, 2015). Despite this, it must be remembered that the lack of influence of turbidity on consumptions rates may indicate that the number of pellets consumed may have been influenced by individual satiation of the novelty of the food item.

While the results show that the presence of turbidity can improve foraging efficiency, our study did not consider other factors that influence foraging. Reacting to the presence or potential presence of predators causes the behaviour of foraging animals to change (Lima and Dill, 1990). For example, olfactory cues from predators reduce the foraging rate of sticklebacks in turbid conditions, but in turbid conditions with no predators, turbidity does not constrain foraging (Webster et al., 2007). Similar results are seen in guppies reared in turbid water, who increase activity when exposed to turbidity but decrease activity when exposed to a predator and turbidity combined (Ehlman et al., 2015). From this, we could infer that the difference between the two species is that *O. niloticus* feels less threatened than *O. amphimelas* in turbid water that has no predator cues. This is an important distinction as the presence of predators could change the behaviour of fish according to the trade-offs they are willing to make in terms of potential growth and mortality. Therefore, future studies of the foraging behaviour of these species should consider manipulating predator cues.

Whether an animal is willing to make a trade-off between a potential foraging gain and potential predation depends on the combination of several traits, including their risk-taking tendency (i.e. boldness). Although this study focused on general foraging efficiency, our data included the impact of turbidity on foraging latency. Latency to an event, most commonly the time taken to leave a shelter, is a common measure of boldness and is influenced by environmental factors including turbidity and natural daytime changes in temperature (Bell, 2005; Biro et al., 2010). Boldness is a personality trait that is consistently different between individuals over time, and is positively linked to increased exploration, activity, risk-taking and food consumption (Sih et al., 2004; Ward et al., 2004). Our results indicate that overall *O. niloticus* is bolder than *O. amphimelas*. If O. *niloticus* are more likely to take risks while exploiting the cover provided by turbidity *O. amphimelas* access to food and could be limited. This combined with the possible hybridisation of both species could seriously impact the population of *O. amphimelas.* We suggest that further investigation into the boldness of both species

should be completed to decern how personality influences the behaviour of individuals and species in response to changing environments.

Our results demonstrate that turbidity positively influences the foraging of *O*. *niloticus* and neutrally impacts the foraging of *O. amphimelas*. The increase in likelihood of *O. niloticus* to first forage in turbid water suggests that it is suited to foraging in limited visibility. This explains the association between O. *niloticus* and degraded habitats and suggests that they can potentially outcompete native species in areas affected by rapid environmental change. Further investigations into boldness and foraging in turbid conditions would help determine how these species balance trade-offs in turbid environments. This is necessary considering the ecosystem-altering behaviour of *O. niloticus*, which can increase levels of turbidity (Linde et al., 2008). Understanding the mechanisms that determine the efficiency of foraging in areas where vision is limited will improve our knowledge of the impacts of environmental change. This study shows that *O. niloticus* forages more efficiently than *O. amphimelas* and that for *O. niloticus* foraging improves as turbidity increases.

The effect of turbidity on risk taking and personality variation of the invasive Nile tilapia, *Oreochromis niloticus,* and the Manyara tilapia *Oreochromis amphimelas*

Abstract

The use of antipredator behaviours in animals is governed by an individual's perception of risk. Perception of risk often varies between individuals who act consistently in response to situations with similar levels of risk. This is used to determine an individual's personality traits and recent studies have highlighted the importance these traits in antipredator behaviour. One such trait is boldness which is linked to activity, feeding rates and susceptibility to predation. To test how risk taking and its repeatability alter in response to turbidity, we recorded the latency to first leave a shelter, the time across the midline of the test tank and the total time outside of the shelter of two cichlid species *Oreochromis niloticus* and *Oreochromis amphimelas* in clear and turbid water. We aimed to investigate whether the visual environment influences individual consistent behaviours, alters risk taking and changes the perception of risk in both species. Our result showed that the latency to first leave the shelter was not influenced by the presence of turbidity. Both species were less likely to cross the midline and spent more time in the shelter in turbid water. Consistent individual behaviour was only expressed by *O*. *amphimelas* when leaving the shelter in turbid water. Our results show that turbid water increases the perception of risk of both species but does not invoke consistent individual behaviours or alter mean boldness.

Keywords: Boldness, repeatability, sheltering, risk, antipredator, personality.

Introduction

Detecting predators is vital to prey survival and influences the decisions of prey (Lima and Dill, 1990). When an animal is performing antipredator behaviour it will inevitably reduce the amount of time it spends foraging or looking for potential mates (Lima and Dill, 1990; Becker et al., 2016). However, not all animals react equally to the same stimuli and inter-individual consistencies in behavioural traits have been identified that indicate a scale of animal temperament (Réale et al., 2007). These consistent behavioural differences have been displayed across a range of taxa, from mammals, birds and fish to spiders and cephalopods (Stamps, 2007). One trait which often determines individual temperament is boldness, which is defined by an individual's inclination towards taking risks (Sloan et al., 1994). Bolder individuals are more likely to put themselves in greater personnel danger in order to receive better rewards, and is positively correlated with activity, exploration and aggression (Mazué, et al., 2015). Bolder individual are more likely to forage in high risk situations, increasing their overall growth rates but also their likelihood of predation (Stamps, 2007). Bolder individuals are also more likely to display repeatable behaviours and adhere to a rigid routine structure which reduces their adaptability in changing or novel environments (Bell et al., 2009). However, individuals may not behave consistently along this continuum between specific contexts, for example displaying variations in boldness in response to a threatening stimulus and non-threatening stimulus, indicating the plastic nature of individual boldness across different situations (Coleman and Wilson, 1998). However, boldness is not the only condition that promotes high risk behaviours and individuals who are in poor a condition are also more likely to respond less effectively to threats (Harding et al, 2020).

Several studies have shown that external factors influence boldness in individuals and populations. Exposure to predation increases aggression in bold sticklebacks, a possible coping mechanism that indirectly influences behaviour towards conspecifics (Bell and Sih, 2007). This can also influence their prey, the boldness of a predator will influence the risk of predation in prey resulting in bolder

predators increasing risk for prey more than shyer predators (Ioannou et al., 2008). This results in boldness being selected for in populations that are historically exposed to greater levels of predation (Fraser and Gilliam, 1987). This has been seen in populations of *Brachyraphis episcopi* residing in areas of high stress, where the selection of a reduced stress response to predators has developed to reduce energy expenditure (Brown et al*.,* 2005). The social composition of groups can alter the boldness of both male and female guppies, who will return to normal movement sooner in the presence of female only shoals than male only shoals (Piyapong et al., 2010). Recent experiences can also influence how bold individuals act and those that have just been exposed to any level of risk are more likely to leave shelters and approach novel objects than those who have not recently been in danger (Darby and McGhee, 2019). The boldness of individuals has also been observed to alter in reaction to environmental change. This can be seen in minor changes of temperature that influence boldness by increasing activity rates of coral reef fish (Biro et al.,2010). Exposure to temperature change and hypoxia also move rainbow trout, *Oncorhynchus mykiss*, towards intermediate boldness, increasing boldness in shy individuals and decreasing it in bolder individuals (Frost et al., 2013). These variations suggest that changes in environment will alter how an individual reacts when considering the cost and benefit of foraging and other activities.

Reduced vision changes an individual's perception of risk in response to an unreliable assessment of their immediate surroundings (Chamberlain and Ioannou, 2019; Ehlman et al., 2019; Gregory, 1993; Kimbell and Morrell, 2015a). Chinook salmon, *Oncorhynchus tshawytscha,* reduce antipredator behaviour in turbid conditions, suggesting a decreased perception of risk (Gregory, 1993). This has also been observed in juvenile perch, *Perca fluviatiilis,* who use vegetation as cover less in turbid conditions (Snickars et al.,2004). Relaxed antipredator behaviour in juveniles is consistent with the effects of turbidity on smaller individuals, who benefit from the cover provided by turbidity but are not visually disadvantaged by it (Utne-Palm, 2002). The disruption of visual cues reduces the

perception of risk as individuals are unable to detect the presence of predators within the immediate area, reducing the need to practice antipredator behaviour (Abrahams and Kattenfeld, 1997).

However, turbidity does not consistently relax antipredator behaviour. The presence of turbidity can reduce activity levels in sticklebacks in the presence of predators and encourage the use of sheltered areas, indicators of an increased perception of risk (Ajemian et al.,2015). Increased antipredator behaviour has also been displayed in the spiny damselfish, *Acanthochromis polyacanthus,* who reduces activity and feeding in turbid conditions in the presence of predator cues (Leahy et al., 2011). The change in the expression of antipredator behaviour can even be within species as turbidity changes. Individuals in turbid conditions that amplify visual ability will have a greater expression of antipredator behaviour as predators will be highlighted against the background (Ehlman et al., 2019; Hinshaw, 1985). This encourages inter-individual consistent behaviours and displays how environmental change can impact the expression of antipredator behaviours (Ehlman et al., 2019). This demonstrates that the perception of risk informs antipredator behaviour and suggests that the combination of multiple stressors will impact individuals in a different way that any singular one. The current literature shows that the presence of turbidity can both enhance and diminish the perception of risk. By understanding how these traits change behavioural reactions to turbidity we can further understand predator-prey interactions and how the environment impacts their behaviour.

We aim to further investigate the relationship between turbidity and the perception of risk. By focusing on the antipredator behaviour of the subject species from the previous experiment, *O. amphimelas* and *O. niloticus*, we can develop a greater insight into the way that turbid conditions influence the behaviour of these species that have importance in freshwater conservation. We measure how turbidity changes the latency to first leave a shelter, a common measure of boldness, as well as the time taken to first cross the midline of the tank and the total time outside the shelter

(Harcourt et al., 2009; Bevan et al., 2018). We will also test whether turbidity increases or decreases consistent repeatable behaviours between individual fish, allowing us to determine if visual disruption changes inter-individual variation. We predict that turbidity will increase the level of risk displayed by *O. amphimelas* and negatively or neutrally impact the level of risk displayed in *O. niloticus*, producing repeatable behaviours in *O. amphimelas* (Ehlman et al., 2019).

Method

Subjects

The fish used in this experiment came from the same stock as the last experiment but none of the same fish were used in both experiments. 29 *O. amphimelas* (65.3 ± 7.5 mm mean ± S.D body length) and 32 *O. niloticus* (79.6 ± 6.9 mm mean ± S.D body length) took part in the experiment, 3 *O. amphimelas* were removed during the trial as they were considered unfit. During routine observation across the trail period, these individuals appeared injured and were removed. It was assumed that this was an instance of aggressive behaviour that is often displayed in cichlids (Chifamba & Mauru, 2017). This resulted in increased monitoring of the other subjects across the trial period but no other injury occurred during the trial. All fish were housed in clear water (0 NTU) in the same 180 litre glass tanks, within the same recirculating system, as the previous fish in the previous experiment. Enrichment items were placed in the holding tanks, including the shelters used in the trials to ensure they were not novel items to the fish during the experiments (Fig. 4). The fish were fed on the same diet as the fish in the previous experiment, the water was kept at the same temperature (26°C) and the same diurnal light cycle (12:12 hours (light: dark)) was used.

Experimental setup

The trials were conducted in the same white acrylic tank with an opaque divider as the previous experiment, and two trials were conducted simultaneously. A shelter created from plastic ornamental plants attached to a white corrugated PVC base was placed in each side of the tank (Fig. 4). Two trials were conducted simultaneously with either two *O. amphimelas* or two *O. niloticus,* one in each half of the arena. The tank was filled with aged water to a depth of 15cm (77.2 litres). All experiments were recorded from above with a Gopro Hero 5 Black at resolution of 1920 x 1080. A white curtain was

drawn across the tank area to reduce disturbances from outside. Trials took place between 18.06.19 and 27.07.2019.

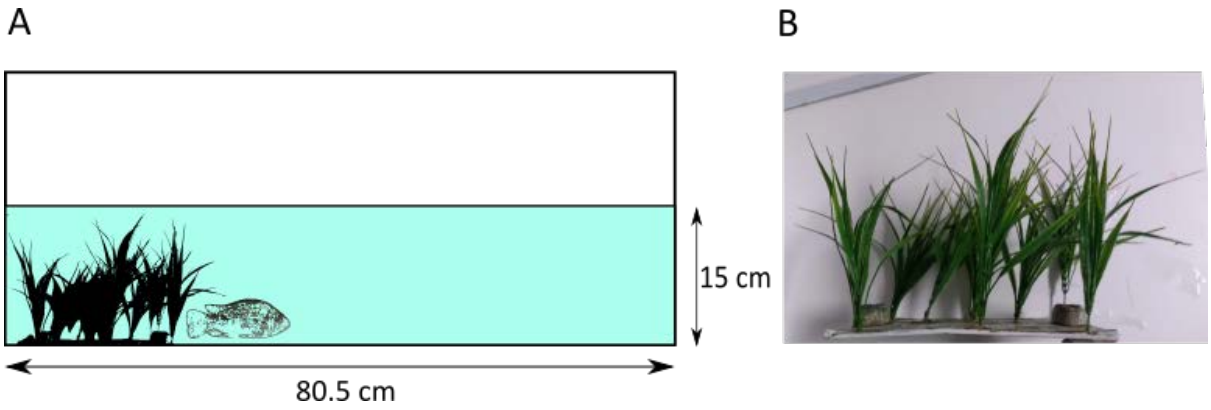

Figure 4. Cross section of one half of the experimental arena showing the position of the plant shelter where the fish were placed at the beginning of the trial (not to scale) (A). Close up photograph of the plant shelter, made from plastic plants fixed to a plastic base and weighted with ornamental rocks (B).

Procedure

16 fish were tested each week, 8 of each species. Each fish took part in one trial per day for 4 consecutive days, in clear (0 NTU) or turbid water (15 NTU). Turbid water (15 NTU) was created using the same procedure as in experiment one (kaolin clay (0.04 mg/l)) and measured with the same Thermo Scientific™ Orion™ AQUAfast AQ3010 turbidity meter. Kaolin clay was mixed in the water until the turbidity matched the desired level of 15 NTU. The day before each 4-day trial block, 16 fish were haphazardly caught (8 *O. niloticus* and 8 *O. amphimelas*), their full body length was measured, they were photographed and were assigned individual identification numbers. Fish were split into 4 groups (2 groups of *O. niloticus* and 2 groups of *O. amphimelas*) which were each housed in the same separate plastic containers (45 x 32 x 25 cm, water depth 15 cm, water volume 21.6 litres) as experiment one for the next 4 days. These containers were filled with aged water which was changed each day with a turbidity level to match the next day's trials. This allowed the fish to be acclimated to the require treatment (at 0 or 15 NTU) for 16 hours before each trial.

Each container group of fish was randomly allocated an order to take part in the experiment each day, then the order of testing fish within each group was also randomised. Consistent differences between individuals within clear and turbid water could be tested by exposing each fish to each treatment twice across the 4-day block. The water was re-stirred before each trial to maintain turbidity levels if required. This was then checked to make sure it was at the desired level (0 or 15 NTU), and the camera recording was started. Fish were placed within the shelters; the curtain was then drawn across the area to ensure the subjects were not disturbed during the trial. Trials lasted for 30 minutes and tested fish were returned to their designated plastic container. Fish were only fed after all individuals had taken part in the day's experiments to standardise hunger during the trials. At the end of the 4-day trial block, test fish were removed and held in tanks of used fish to avoid individuals being used more than once. BORIS software version 7.7.3 was used to analyse the videos and record the latency of the fish to first leave the shelter, the time taken for the fish to first cross the midline of the tank after leaving the shelter and the total time that the fish spent out of the shelter (Friard and Gamba, 2016). This was completed by one individual to maintain consistency. All protocols were approved by the University of Bristol Ethical Review Group, UIN/UB/18 067.

Statistical analysis

Analysis was performed with R version 3.5.3 (R Core Team, 2019). The censored time-to-event response variables, i.e. the latency to first leave the shelter and the latency to first cross the midline, were analysed with survival analysis. Schoenfeld residuals, deviance residuals and dfbeta outliers showed no variation over time meeting the assumptions of unaltered survival analysis. The complete data was first analysed to allow the effects between species to be determined, then it was split by species to determine the effect of turbidity within each species.

The total time spent outside the shelter was analysed with a generalised linear mixed model (GLMM) with a Poisson distribution as the assumptions for Gaussian models were not met. The model included an interaction between species and turbidity and their main effects, a continuous variable (body length) and a categorical variable (arena side). Models were also created for each species separately including categorical (turbidity and arena side) and continuous (body length) variables and a random effect (Fish ID). To reduce overdispersion, turbidity and body length were scaled and an observation-level random effect term was included in the model (Harrison, 2014). Likelihood ratio tests were used to remove non-significant interactions by deleting terms based on chi squared tests with the "drop 1" function.

To assess the consistency of inter-individual variation for each of the three response variables Spearman rank non-parametric correlation tests were used. These were used as Shapiro-Wilk normality tests showed the data was not normally distributed ($P < 0.05$) and the censored data for the two latency response variables can lead to spurious estimates of formal repeatability scores (Ioannou and Dall, 2016; Stamps et al., 2012).

Results

Cox proportional hazards (CPH) showed that the likelihood of leaving the shelter for the first time did not differ between species (CPH: Hazard ratio (HZ) = 1.01, N = 244, *P* = 0.9). The likelihood of leaving the shelter was not significantly different between treatments for either species (*O. amphimelas*: CPH: HZ = 0.68, N = 116, *P* = 0.06; *O. niloticus*: CPH: HZ = 0.73, N = 128, *P* = 0.1; Fig. 2). The likelihood of crossing the midline for the first time did not differ between species (CPH: HZ = 0.68, N = 244, *P* = 0.1). However, the likelihood of crossing the midline was significantly lower in high turbidity (15 NTU) than clear water for both species (*O. amphimelas*: CPH: HZ = 0.51, N = 116, = 0.001; *O. niloticus*: CPH: HZ = 0.57, N = 128, *P* = 0.003; Fig. 5).

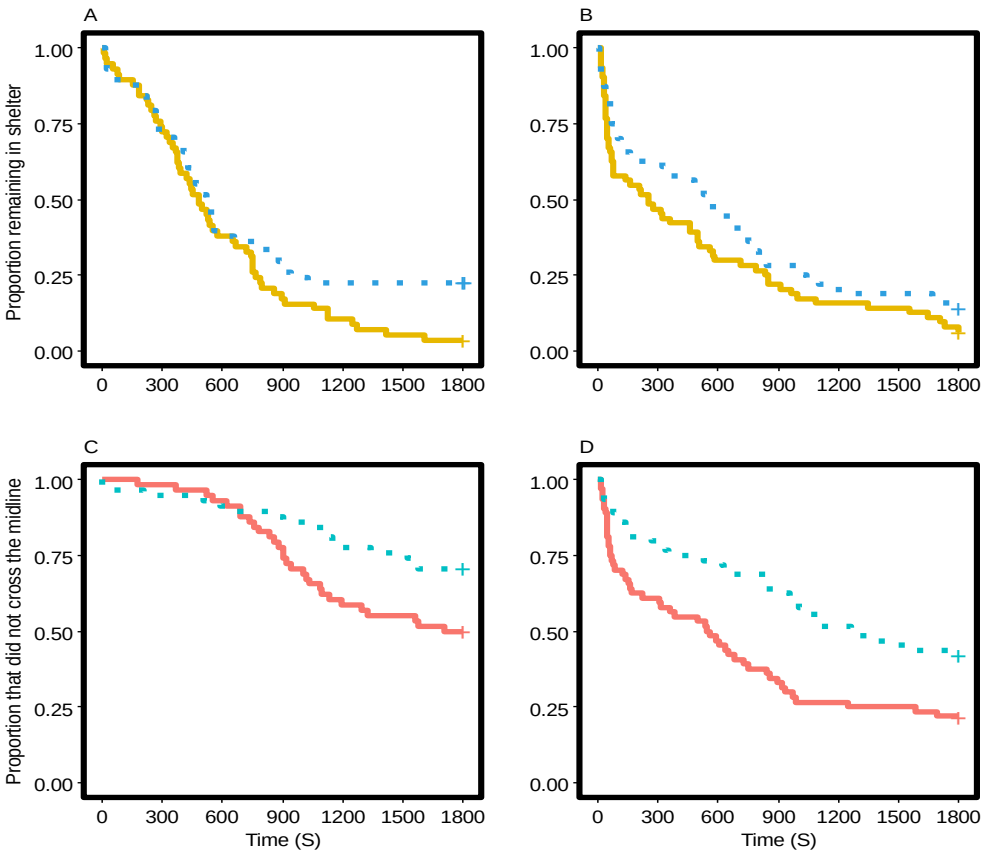

Figure 5. Kaplan-meier event estimates displaying the proportion of individuals to first leave the shelter (A) O. amphimelas and (B) O. niloticus as well as crossing the midline for the first time (C) O amphimelas and (D) O. niloticus, in both 0 NTU (solid) and 15 NTU (dotted) treatments.

The interaction of species and turbidity had no impact on the total time spent outside the shelter (GLMM: species * (scale(turbidity)): $\chi^2_1 = 0.33$, $P = 0.5$). The total time outside of the shelter did not differ between species (GLMM: species $\chi^2_1 = 0.53$, $P = 0.4$; Fig. 6). The total time outside the shelter was shorter in turbid water for both *O. amphimelas* (GLMM: (scale(turbidity)) $\chi^2_1 = 10.85$, $P = 0.0009$; Fig. 3) and *O. niloticus* (GLMM: (scale(turbidity)) $\chi^2_1 = 10.23$, $P = 0.001$; Fig. 6).

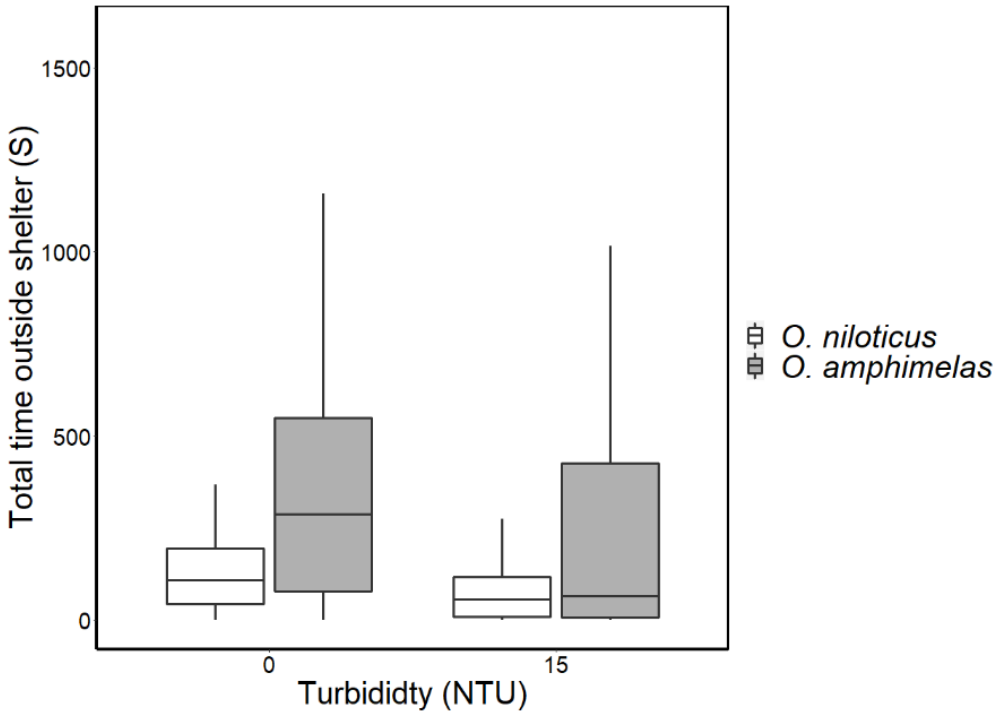

Figure 6. Total time spent outside the shelter. The median are horizontal lines within the boxes, the interquartile range is the area within the boxes and the whiskers display the data within 1.5 x IQR.

Spearman rank correlation coefficients showed inter-individual consistency in the latency of *O. amphimelas* to first leave the shelter in the 15 NTU treatment but no significance was seen in any of the other correlation coefficients (N = 29, $r_s = 0.405$, $P = 0.029$; Table 1), this suggests that little evidence of consistent inter-individual variation was displayed in either species.

Table 1 Spearman's rank correlation coefficients (rs) for behaviours measured in two repeated trials in clear and turbid water. 29 O. amphimelas and 32 O. niloticus were tested. Significant values are shown in bold.

	Turbidity (NTU)	r_s	*p*
Latency to first leave shelter *O. amphimelas*	0	0.044	0.817
	15	**0.405**	**0.029**
Latency to first leave shelter *O. niloticus*	0	0.037	0.836
	15	0.094	0.607
Latency to first cross midline *O. amphimelas*	0	0.126	0.513
	15	-0.292	0.123
Latency to first cross midline *O. niloticus*	0	0.088	0.629
	15	0.040	0.827
Total time outside shelter *O. amphimelas*	0	-0.201	0.293
	15	0.347	0.064
Total time outside shelter *O. niloticus*	0	-0.143	0.432
	15	0.088	0.629

Discussion

We predicted that turbidity would have a more profound effect on the boldness of *O. amphimelas* than *O. niloticus*. This would be expressed by *O. amphimelas* taking longer to leave the shelter, crossing the midline later and spending more time in the shelter than *O. niloticus* as measures of increased risk taking. Our results show that turbidity did not change the latency to first leave the shelter, the time taken to first cross the midline or the total time outside of the shelter between both species. Our results do show that the presence of turbidity did not change the likelihood of either species to leave the shelter but reduced the time both species crossed the midline of the tank. Both species spent more time within the shelter in the turbid treatment. These results also indicate that the presence of turbidity increases the perception of risk of both species outside of the shelter possibly as a consequence of reduced visibility. Consistent inter-individual behaviour was only displayed by *O. amphimelas* when leaving the shelter in 15 NTU. The lack of overall change in latency to leave the shelter for the first time indicates that the turbidity turbid treatment did not change the initial boldness of either species. However, as some individually consistent behaviours were displayed in *O. amphimelas* the presence of turbidity highlights some difference between shy and bold individuals, that is not apparent with O. *niloticus*.

The influence of turbidity on the boldness of both species was similar. Firstly, turbidity's lack of impact on the latency to first leave the shelter indicates that the initial perception of the risk within and outside of the shelter was similar in clear and turbid water. This conflicts with many studies on turbidity which show that the perception of risk will either increase or decrease in turbid water as a result of reduced visibility (Gregory, 1993; Ehlman et al., 2019a; Lehtiniemi et al., 2005; Chamberlain and Ioannou, 2019). Our results show that the risk perception of both species was unchanged by the presence of turbidity. This could indicate that neither species vision was interrupted sufficiently in the turbid treatment to alter the level of potential risk within the environment. However, an increase in

the time taken to first cross the midline as well as spending more time in the shelter in the turbid treatments shows that the exploration of novel environments is reduced in turbid water. This suggests that the turbid treatment does reduce the risk perception of both species when outside the shelter. These mixed results highlight a flaw in the experimental design concerning the use of latency to first leave a shelter as a measure of risk perception. As the fish were easily able to return to the shelter if they perceived risk throughout the trial period leaving the shelter only indicates that the area immediately outside the shelter is low risk. Future work should ensure that the latency to first to leave the shelter is combined with other measures. As well as the measures used in this study others have used activity level, changes in distribution, latency to decision making and the avoidance of turbid areas to indicate risk (Suriyampola et al., 2018; Gregory, 1993; Chamberlain and Ioannou, 2019; Boubée et al., 1997).

Previous studies have shown how mean behavioural responses can be influenced by external changes in the environment. Low light levels increase the boldness of fish adapted to low light when exploring in low light environments (Kareklas et al., 2016). Fish reared in areas rich in dissolved oxygen and high turbidity showed less risk taking in clear and well oxygenated water suggesting that combinations of environmental factors influence how risk will be perceived (Oldham et al., 2018). This response was so strong it was identifiable in each populations progeny when reared in similar conditions (Oldham et al., 2018). Small changes in temperature influence the boldness of individuals, resulting in fish that previously behaved shyly potentially performing bolder than a bold fish in warmer water (Biro et al., 2010). Hypoxia also changes the boldness of fish and reduces the likelihood of extreme bold and shy behaviours occurring suggesting that behaviours at either end of the scale are not as favoured in extreme situations (Frost et al., 2013). Even the presence of predators can encourage the selection of bold individuals who are more likely to take risks under the pressure of predation (Fraser and Gilliam, 1987).

Although our results suggest that visual limitation reduces risk taking for both species of fish there was little evidence of individual repeatable behaviours that would indicate that turbidity changes the boldness of either species. However, *O. amphimelas* did display a mildly positive correlation in the latency to first exit the shelter in the turbid treatment. This does show some indication of a consistent shy-bold continuum within *O. amphimelas* and suggests that some individuals are bolder than others in turbid water. Although the lack of similar results of behaviours once outside the shelter make these only suggestive, and that personality variation in boldness was weak in the species used compared to other fish that have been tested (Ioannou and Dall, 2016; Bevan et al., 2018; Brown et al., 2005; Biro et al., 2010; Ehlman et al., 2019a). This lack of repeatability could indicate that both species exhibit more behavioural plasticity to changing environments than other species (Frost et al., 2013; Ehlman et al., 2019). This is consistent with observations of *O. niloticus* that associate it with turbid conditions and navigate using non-visual sensory mechanisms displaying its plasticity to a wide range of environments (Linde-Arias et al., 2008; Zhang et al., 2017; Marusov and Kasumyan, 2017). Although O. *amphimelas* may be more behaviourally plastic than other native species, allowing it to adapt to small variations in turbidity, the combination of multiple stressors such as the presence of *O. niloticus* could result in increased pressure that results in the decline of the species (Bauer, 2012). Further investigation should be conducted into the risk taking of both species at a range of turbidity to determine its impact.

Past work into individual repeatable behaviours show that individuals who display consistent behavioural types will have limited behavioural plasticity when exposed to changing environments (Sih et al., 2012). These individual differences in boldness are ecologically important as bolder individuals are more likely to feed, maximizing growth rates, while being exposed to a greater predation risk (Webster et al., 2007; McDonald et al., 2016; Stamps, 2007). The perception of risk increases the repeatability of behaviours and fish in turbidity levels similar to this study exhibit strong

antipredator responses when also exposed to predator cues (Ehlman et al., 2019). A number of other studies have investigated the effects of turbidity and the presence of predators on fish and suggest that the combination of predators and environmental change influences risk perception (Pekcan-Hekim et al., 2006; Figueiredo et al., 2016; Gregory, 1993). Future studies may consider the use of predator cues or other indications of risk, such as avian models above the arena or simulated attacks to drive subjects into cover, to increase the perceived perception of risk.

Our results suggest that both species of fish had a higher perception of risk when outside the shelter than in turbid water. This is expressed through reduced time spent in the open turbid water and an increase in the time taken to cross the midline of the tank. Reduced visibility has been attributed to heightening risk perception and increasing the time that individuals take to make decisions while foraging (Chamberlain and Ioannou, 2019). Conversely turbidity has been seen to constrain the ability of fish to assess risk, increasing the likelihood of being predated upon (Sohel and Lindström, 2015). Turbid water also increases the use of sheltered habitats in response to predation, possibly a result of the combination of reduced visibility and increased risk of predation driving individuals into sheltered areas (Ajemian et al., 2015). Other studies have identified turbidity as providing shelter for fish and reducing the perception of risk proposing the “turbidity as cover hypothesis” (Gregory and Northcote, 1993). This negates the use of sheltered areas as cover from predation as cover is provided from the turbid open water. This is demonstrated in Snickars et al., (2004) where the importance of dense vegetation as cover reduces as turbidity increases. However, there is a reason that potentially explain why neither species in this study conform to the “turbidity as cover hypothesis”. The turbidity treatment used in this study was relatively low compared to other studies and the effects of turbidity as cover may be relevant to both species beyond a threshold higher than the one tested.

We have shown that reduced visibility increases the perception of risk of both species of fish and encourages shelter use. We were unable to find any substantial individual consistent behaviours (personality variation), particularly in clear water. This could possibly be a result of the limitations of the experimental design, as a low level of turbidity was used in the study and the potential risk of predation was not increased beyond the reduction of visibility. Further research into the behavioural differences between species in response to environmental change will increase our understanding of the effects of anthropogenic change and will allow the impact of turbidity to be mitigated. Our results indicate that the presence of turbidity can encourage shelter use in both species tested, while not inducing individual consistent behaviours.

Discussion

The results of both experiments suggest that the presence of low levels of turbidity (< 15 NTU) cause similar behavioural reactions in both species, increasing the perception of risk and showing some increase in foraging efficiency. However, as turbidity increases further (from 15 to 30 NTU), the foraging efficiency of *O. amphimelas* reduces and the foraging efficiency of *O*. *niloticus* continues to increase. This, combined with the fact that the food consumption of *O*. *niloticus* was greater across all treatments suggests that even in the absence of turbidity, *O*. *niloticus* could threaten *O. amphimelas* through competition over food. This could have ecological importance as populations of these species are now sympatric in the wild and a human-driven increase in turbidity could further increase the competitive pressure put upon *O. amphimelas* (Shechonge et al., 2019). The lack of inter-individual consistent personality variation in either species does indicate behavioural plasticity is not limited to turbid conditions. This may indicate that *O. amphimelas* could potentially adapt to turbid environments but in the presence of the more adept forager, *O*. *niloticus*, this limited behavioural flexibility may not be adequate. As many invasive species are known to rapidly adapt to new or degraded environments, investigating the impact of environmental change combined with the presence of invasive species will allow a greater understanding of potential threats to native biodiversity (Mainka and Howard, 2010; Hazelton and Grossman, 2009a). This is especially important considering the role of some invasive species in increasing turbidity (Zhang, Mei and Gulati, 2017; Zambrano and Hinojosa, 1999), suggesting they may change the local habitats too quickly for native species to adapt (MacDougall and Turkington, 2005). Our study suggests that although *O. amphimelas* may be able to adapt to low levels of turbidity, rising levels and the presence of competitors could lead to their decline. To effectively mitigate the effect of reduced vision on the behaviours of threatened native species, we must first understand how the visual capability of fish inform their behaviour.

The degree to which an animal is affected by the visual disruption caused by turbidity is dependent on their visual acuity, described by Caves et al. (2017) as "the ability to resolve spatial detail". Caves et al. (2017) go on to describe this ability to be most adept in larger clearwater species and those found in complex habitats, and turbid water species having reduced acuity due to their reduced eye and body size rather than as an adaption to disrupted vision. This suggests that species adapted to turbid water do not need better eyesight than those in clear water but instead compensate for reduce vision. This could be especially true at low levels of turbidity, displayed in our results through a peak of foraging efficiency for *O. amphimelas* at 15 NTU, where the presence of turbidity actually increases the ability of fish to resolve spatial detail and increases the number of feed attempts (Hinshaw, 1985; Ehlman et al., 2019). However, as turbidity rises, other senses need to be utilised as objects are no longer highlighted against the background, forcing fish to rely more on chemoreceptive cues to inform them on the presence of food, conspecifics and predators (Ferrari and Chivers, 2006; Hiermes et al., 2015; Lunt and Smee, 2015).

The limit of a species visual ability are important ecologically, as species with high visual acuity and those native to clear water or highly complex habitats are the most vulnerable to fluctuations in turbidity (Johansen and Jones, 2013; Wenger et al., 2013; Caves et al., 2017). For examples in coral reefs, which are habitats that have high water clarity and are complex, the presence of suspended sediment could also restrict olfactory cues further reducing the ability of species to adapt to turbid conditions (Wenger et al., 2011). The upkeep of clear water and complex habitats is important to visually dependant species so preserving natural levels of water clarity could be as important as other parameters of water quality. However, developmental plasticity often occurs in response to long-term adaptations by individuals and populations that are exposed to differing environmental conditions during development (Stamps and Groothuis, 2010; Ehlman et al., 2015). Long term differences between habitats, including changes in visibility, temperature and predation risk, favours the selection

of behaviours most suited to that environment (Brown et al., 2005; Abrahams, Mangel and Hedges, 2007). This can be seen in fish reared in differing levels of turbidity which switch from visual to olfactory cues as a primary way to detect food and navigate (Chapman et al., 2010). This suggests that chronic exposure to low levels of turbidity may be less damaging to *O. amphimelas* than a point source event that raises turbidity quickly. A sudden increase in turbidity has been shown to alter behaviours immediately and could potentially result in *O. amphimelas* being restricted when gathering food during reproduction (Gray, Sabbah and Hawryshyn, 2011).

This is where the role of *O. niloticus* in creating turbid environments where it has been introduced may become problematic for native species (Zhang, Mei and Gulati, 2017). If the presence of *O. niloticus* is linked to a rise in turbidity it would suggests that native species have to compete in unnatural conditions with a fish that is more adapted to these conditions than themselves. However, the similar increase in risk perception as *O. amphimelas* in relatively low levels of turbidity suggests that *O. niloticus* may not have an extreme effect on the degradation of a habitat. Instead *O. niloticus* may have the characteristic of a "backseat driver" invasive species, taking advantage of partially degraded habitats and further degrading them while native species decline from a combination of degraded habitats and intra-species competition (Mainka and Howard, 2010; Bauer, 2012). This differs from invasive species described as "drivers" whose introduction lead to alterations in the ecosystems they are introduced into which change its function (Vitousek et al., 1987). Distinguishing the status of *O. niloticus* as either a backseat driver or a driver is important as it determines whether the management strategy in dealing with their introduction should focus on preventing initial environmental degradation or physical removal of the pest (Bauer, 2012). As dominant invasive fish outcompete native individuals while foraging in turbid water, investigating the relationships between the tolerance of turbidity, foraging ability and consistency of inter-individual variation will allow a greater understanding on the impact of the complicated relationship between environmental change, invasive species and native populations (Hazelton and Grossman, 2009a).

Our experiments indicate that both species' behaviours are influenced by the presence of food in the trial arena. This can be seen in how the behaviours of both species expressed change between experiments. In the case of *O. niloticus*, turbidity did increase its ability to forage, suggesting that antipredator behaviours were not increased and the perceived level of risk was low, however in turbid water without the presence of food, *O. niloticus* increased its sheltering behaviour suggesting an increased perception of risk. Examples such as this indicate how context influences the behavioural trade-offs made by animals and encapsulates the motivations that govern the balance between foraging and antipredator behaviour (Lima and Dill, 1990). *O. amphimelas* feeding less in the highest turbidity and increasing refuge use in turbid water suggests that the combination of *O. niloticus* and turbid water would be disadvantageous for *O. amphimelas* as it would be unable to compete when foraging.

The reduced antipredator behaviour in the first experiment in turbid conditions may have been a consequence of the fact that no shelter was available for fish to obviously shelter in. However, the sensory environment of the experimental arena may influence the behaviour of the fish and lead to differences in antipredator behaviour between experiments. Hale et al. (2009) displayed that cues that inform behaviours can differ depending on the source of the medium that the cues travels through (i.e. water) and may change depending on time, flow and pollution. This may result in individuals avoiding or be drawn to patches that appear beneficial due to the presence of food cues, or the absence of predator cues (Brodin et al., 2006). This has resulted in questioning the importance of the detection of olfactory cues in non-natural experimental water which provide stronger responses to olfactory cues than in natural water (Hale et al., 2009). This could not only apply to the accuracy of experimental water compared to the natural water but behavioural responses could also be influenced by other factors not tested. However, considering these fish were bred in captivity and the water used was part of the same system that housed them, it seems reasonable that these conditions are least natural to the fish that were tested. Future studies should consider the range of multiple

cues in water that are constantly informing fish and investigate the implications of varying conditions between lab and *in situ* experiments.

These implications produce questions concerning the combination of turbidity and invasive competition for *O. amphimelas*. For example, would either species forage differently in turbid water in the presence conspecifics or in the presence of predators? Earlier studies have indicated that turbidity increases the perception of threat and reduces social cohesion of groups resulting in reduced group size or a lack of groups forming in turbid conditions (Chamberlain and Ioannou, 2019; Kimbell and Morrell, 2015b). Maintaining group size is a common defence against predation so one might assume that turbidity's impact in constraining aggregation would increase susceptibility to predation (Krause et al., 2002). However, the feeding behaviour of predators who rely on sight is also affected, reducing the likelihood of prey encounters and consumption rate in turbid water (Turesson and Brönmark, 2007). This reduces the selection of specific prey species so as to increase the probability of capturing any prey encountered (Snow, Shoup and Porta, 2018). Therefore, the visual restriction created by turbidity may instead benefit prey species by reducing encounter rates while the perception of threat is still high, as prey themselves are also disadvantaged and unable to anticipate whether a predator is present.

Studies have indicated that increasing the perception of risk reduces foraging efficiency, so high turbidity would constrain the food consumption of both species mechanistically as well as through increasing the time being spent performing antipredator behaviour (Figueiredo et al., 2016). Recent work has also identified *O. niloticus* exhibiting agonistic behaviour more quickly than *O. amphimelas* and displaying dominance in their competitive interactions (Champneys, Genner and Ioannou, 2020). Investigating similar behaviours in turbid conditions could potentially reveal the effect of turbidity on the level of agonistic behaviour between the two species. As an increase in sheltering in turbid water was observed, *O. niloticus* may react by increasing agonistic behaviour towards *O. amphimelas* to

inhabit the best shelter for their own protection. Investigating interactions such as these will provide a valuable insight into how environment change influences the interactions between invasive and native species.

Inter-individual consistent behavioural variation can explain the limited plasticity displayed when individuals respond to changing environments (Kareklas et al., 2016; Réale et al., 2007). Individuals are limited to react consistently as the environment changes, for example bolder individuals have rigid and more routine behaviours than shyer individuals who are more flexible in response to environmental change (Jolles et al., 2019). One idea for the occurrence of Inter-individual consistent behaviours is thought to be the increased benefit in consistently performing similar behaviours in similar situations that are able to increase fitness (Wong et al. 2013). This can be seen in bolder individuals who increase grow rates at a faster rate than shyer individuals due to their bold behaviour increasing their likelihood of feeding occurring (Stamps, 2007). Our study displayed that little inter-individual consistent behaviour were expressed in either species which indicates that personality variation is less apparent than in other observed fish species (Bevan et al., 2018; Szopa-Comley, Donald and Ioannou, 2020). This suggests that neither species appears to benefits from acting consistently in the second experiment even though the perceived level of threat was higher in turbid than in clear water. This may indicate that although the perception of threat was higher in turbid water, it is not yet high enough to demand consistent reactions that may improve fitness, allowing both species to react more adaptably until this threshold is reached. However, this behavioural flexibility can be costly in an continuously changing environment, as changing behaviour to suit a local environment increases the uncertainty of the surrounding environment, increasing the likelihood of responding unsuitably overall (Dall, Houston and McNamara, 2004).

Further complicating the relationship between turbidity and behaviour is the difference in visual disruption from different types of turbidity. Algal induced turbidity has more of a visual impact on fish

species than clay induced turbidity (Quesenberry et al., 2007; Webster et al., 2007; Sohel et al., 2017; Radke and Gaupisch, 2005b; Li et al., 2013). The disparity between these types of turbidity has been attributed to organic and inorganic particles scattering light at different intensities and disrupting visibility to different degrees (Lythgoe, 1979). Eutrophication resulting in algal turbidity will have a more profound behavioural impact on visually dependant fish than sedimentation from increased runoff or substrate resuspension. This is concerning due to the increase of eutrophication globally, especially in developing countries (Le et al., 2010; Jeppesen et al., 2012). However, the role of *O. niloticus* in encouraging algal turbidity is still unclear as studies show that *O. niloticus* can encourage phytoplankton growth by increasing nutrients but also limit it through grazing (Starling et al., 2002; Torres et al., 2016). As the impact of algal turbidity is greater than sediment resuspension, *O. amphimelas* and other threatened native species that are exposed to eutrophication may be more vulnerable to the introduction of invasive species. As this study only investigated the effects of clay turbidity on behaviour, further examining the role of algal turbidity on fish behaviour would give greater insight into the impact of species associated with degraded habitats.

Our experiments have indicated that turbid water changes the behaviour of both *O. niloticus* and *O. amphimelas*. They highlight that the effect of turbidity on fish is complex and varies across species and contexts. They also show how the combination of the introduction of a turbidity tolerant species with an increase in turbidity may exert extra pressure on threatened native species. However, our prediction that *O. niloticus* would be consistently more suited to turbid conditions was not supported. As both species displayed a similar level of risk in the intermediate turbid treatment with no food, the impact of *O. niloticus* on native species may be less extreme than initially thought. However, the fact that *O. niloticus* forages more effectively in turbid water and consumes more than *O. amphimelas* regardless of turbidity level suggests that it could be a real threat through competition over food. Investigating repeatable inter-individual behaviours in wider ranges of turbidity with food or conspecific cues would allow conformation of the results concerning the lack of inter-individual

behaviours. Natural environments are filled with complex combinations of cues (Hale et al., 2009), so investigating how combinations of cues influence fish behaviour will give us a greater insight into how environmental change alters ecosystems.

References

Abrahams, M. and Kattenfeld, M., 1997. The role of turbidity as a constraint on predator-prey interactions in aquatic environments. *Behavioral Ecology and Sociobiology*, 40, pp.169–174.

Abrahams, M. V., Mangel, M. and Hedges, K., 2007. Predator-prey interactions and changing environments: Who benefits? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362, pp. 2095–2104.

Ajemian, M.J., Sohel, S. and Mattila, J., 2015. Effects of turbidity and habitat complexity on antipredator behavior of three-spined sticklebacks (*Gasterosteus aculeatus*): Antipredator behavior in sticklebacks. *Environmental Biology of Fishes*, 98, pp.45–55.

Andersen, M., Jacobsen, L., Grønkjær, P. and Skov, C., 2008. Turbidity increases behavioural diversity in northern pike, *Esox lucius L.*, during early summer. *Fisheries Management and Ecology*, 15, pp.377–383.

Andree, S.R. and Wahl, D.H., 2019. Effects of turbidity on foraging of juvenile black and white crappies. *Ecology of Freshwater Fish*, 28(1), pp. 123-131.

Barrett, J.C., Grossman, G.D. and Rosenfeld, J., 1992. Turbidity-Induced Changes in Reactive Distance of Rainbow Trout. *Transactions of the American Fisheries Society*, 121(4), pp.437–443.

Bauer, J.T., 2012. Invasive species: 'back-seat drivers' of ecosystem change? *Biological Invasions*, 14(7), pp.1295–1304.

Becker, L.J.S., Brooks, E.M., Gabor, C.R. and Ostrand, K.G., 2016. Effects of Turbidity on Foraging Behavior in the Endangered Fountain Darter (*Etheostoma fonticola*). *The American Midland Naturalist*, 175(1), pp.55–63.

Becker, R.A., Chambers, J.M. and Wilks, A.R., 1989. The New S Language. *Biometrics*.

Bell, A.M., 2005. Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *Journal of Evolutionary Biology*, 18, pp.464–473.

Bell, A.M., Hankison, S.J. and Laskowski, K.L., 2009. *The repeatability of behaviour: a meta-analysis*. *Animal Behaviour*,77(4), pp.771-783.

Bell, A.M. and Sih, A., 2007. Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters*,10(9), pp. 828-834.

Benfield, M.C. and Minello, T.J., 1996. Relative effects of turbidity and light intensity on reactive distance and feeding of an estuarine fish. *Environmental Biology of Fishes*,46, pp.211-216.

Bevan, P.A., Gosetto, I., Jenkins, E.R., Barnes, I. and Ioannou, C.C., 2018. Regulation between personality traits: Individual social tendencies modulate whether boldness and leadership are correlated. *Proceedings of the Royal Society B: Biological Sciences*, 285(20180829.).

Biro, P.A., Beckmann, C. and Stamps, J.A., 2010. Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proceedings of the Royal Society B: Biological Sciences*, 277, pp.71–77.

Bleckmann, H. and Zelick, R., 2009. *Lateral line system of fish. Integrative zoology*.

Bonnet, B.R.P., Ferreira, L.G. and Lobo, F.., 2008. Water quality and land use relations in goias: a watershed scale analysis. *Revista Arvore*, [online] 32, pp.311–322. Available at: <http://www.scielo.br/scielo.php?pid=S0100-67622008000200014&script=sci_arttext>.

Borner, K.K., Krause, S., Mehner, T., Uusi-Heikkilä, S., Ramnarine, I.W. and Krause, J., 2015. Turbidity affects social dynamics in Trinidadian guppies. *Behavioral Ecology and Sociobiology*, 69, pp.645–651.

Boubée, J.A.T., Dean, T.L., West, D.W. and Barrier, R.F.G., 1997. Avoidance of suspended sediment by the juvenile migratory stage of six New Zealand native fish species. *New Zealand Journal of Marine and Freshwater Research*, 31(1), pp.61–69.

Boughman, J.W., 2001. Divergent sexual selection enhances reproductive isolation in sticklebacks. *Nature*,411(6840), pp.944-948.

Brasington, J. and Richards, K., 2000. Turbidity and suspended sediment dynamics in small catchments in the Nepal Middle Hills. *Hydrological Processes*,14(14), pp. 2559-2574.

Brodin, T., Johansson, F. and Bergsten, J., 2006. Predator related oviposition site selection of aquatic beetles (*Hydroporus spp.*) and effects on offspring life-history. *Freshwater Biology*,51(7), pp. 1277-1285.

Brown, C., Gardner, C. and Braithwaite, V.A., 2005. Differential stress responses in fish from areas of high- and low-predation pressure. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, 175, pp. 305–312.

Brown, C., Jones, F. and Braithwaite, V., 2005. In situ examination of boldness-shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. *Animal Behaviour*, 70(5), pp. 1003–1009.

Brydges, N.M. and Braithwaite, V.A., 2009. Does environmental enrichment affect the behaviour of fish commonly used in laboratory work? *Applied Animal Behaviour Science*, 118(3–4), pp. 137–143.

Carter, M.W., Shoup, D.E., Dettmers, J.M. and Wahl, D.H., 2010. Effects of Turbidity and Cover on Prey Selectivity of Adult Smallmouth Bass. *Transactions of the American Fisheries Society*, 139(2), pp. 353–361.

Caves, E.M., Sutton, T.T. and Johnsen, S., 2017. Visual acuity in ray-finned fishes correlates with eye size and habitat. *Journal of Experimental Biology*, 220(Pt 9), pp. 1586–1596.

Chamberlain, A.C. and Ioannou, C.C., 2019. Turbidity increases risk perception but constrains

collective behaviour during foraging by fish shoals. *Animal Behaviour*, 156, pp.129–138.

Chambers, J.M., 2017. Linear models. In: *Statistical Models in S*. Routledge, pp.95–144.

Champneys, T., Genner, M.. and Ioannou, C.C., 2020. Invasive Nile tilapia dominates a threatened indigenous tilapia in competition over shelter. *H*ydrobiologia. DOI: https://doi.org/10.1007/s10750-020-04341-8

Chapman, B.B., Morrell, L.J., Tosh, C.R. and Krause, J., 2010. Behavioural consequences of sensory plasticity in guppies. *Proceedings of the Royal Society B: Biological Sciences*, 277, pp.1395–1401.

Chifamba PC, Mauru T (2017) Comparative aggression and dominance of Oreochromis niloticus (Linnaeus, 1758) and Oreochromis mortimeri (Trewavas, 1966) from paired contest in aquaria. Hydrobiologia. 788, pp. 193–203

Chivers, D.P., Al-Batati, F., Brown, G.E. and Ferrari, M.C.O., 2013. The effect of turbidity on recognition and generalization of predators and non-predators in aquatic ecosystems. *Ecology and Evolution*, 3(2), pp.286–277.

Chivers, D.P., Mirza, R.S., Bryer, P.J. and Kiesecker, J.M., 2001. Threat-sensitive predator avoidance by slimy sculpins: Understanding the importance of visual versus chemical information. *Canadian Journal of Zoology*,79(5), pp.876-873.

Coleman, K. and Wilson, D.S., 1998. Shyness and boldness in pumpkinseed sunfish: Individual differences are context-specific. *Animal Behaviour*, 56(4), pp. 927-936.

Collin, S.P. and Hart, N.S., 2015. *Vision and photoentrainment in fishes: The effects of natural and anthropogenic perturbation*. *Integrative Zoology*,10(1), pp. 15-28.

Croy, M.I. and Hughes, R.N., 1991. The influence of hunger on feeding behaviour and on the acquisition of learned foraging skills by the fifteen-spined stickleback, *Spinachia spinachia* L. *Animal Behaviour*, 41(1), pp.161–170.

Dall, S.R.X., Houston, A.I. and McNamara, J.M., 2004. *The behavioural ecology of personality: Consistent individual differences from an adaptive perspective*. *Ecology Letters*,7(8), pp 734-739.

Darby, N.A. and McGhee, K.E., 2019. Boldness is affected by recent experience with predation cues and body size in mosquitofish. *Behavioural Processes*,164, pp 143 - 149.

Davies-Colley, R.J. and Smith, D.G., 2001. Turbidity, suspended sediment, and water clarity: A review. *Journal of the American Water Resources Association*, 37(5), pp.1085–1101.

Duffield, C. and Ioannou, C.C., 2017. Marginal predation: Do encounter or confusion effects explain the targeting of prey group edges? *Behavioral Ecology*,28(5), pp. 1283-1292.

Dugas, M.B. and Franssen, N.R., 2011. Nuptial coloration of red shiners (*Cyprinella lutrensis*) is more intense in turbid habitats. *Naturwissenschaften*,98(3), pp. 247-251.

Eaton, L. and Sloman, K.A., 2011. Subordinate brown trout exaggerate social signalling in turbid conditions. *Animal Behaviour*,81(3), pp. 603-608.

Ehlman, S.M., Halpin, R., Jones, C., Munson, A., Pollack, L. and Sih, A., 2019. Intermediate turbidity elicits the greatest antipredator response and generates repeatable behaviour in mosquitofish. *Animal Behaviour*, 158, pp.101–108.

Ehlman, S.M., Sandkam, B.A., Breden, F. and Sih, A., 2015. Developmental plasticity in vision and behavior may help guppies overcome increased turbidity. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 12, pp.1125–35.

Engström-Öst, J. and Candolin, U., 2007. Human-induced water turbidity alters selection on sexual displays in sticklebacks. *Behavioral Ecology*, 18(2), pp. 393-398.

Erftemeijer, P.L.A., Riegl, B., Hoeksema, B.W. and Todd, P.A., 2012. Environmental impacts of dredging and other sediment disturbances on corals: A review. *Marine Pollution Bulletin*, 64(9), pp.1737–1765.

Erftemeijer, P.L.A. and Robin Lewis, R.R., 2006. Environmental impacts of dredging on seagrasses: A review. *Marine Pollution Bulletin*,52(12), pp.1553-1572.

Eriksson, B.K., Sandström, A., Isæus, M., Schreiber, H. and Karås, P., 2004. Effects of boating activities on aquatic vegetation in the Stockholm archipelago, Baltic Sea. *Estuarine, Coastal and Shelf Science*, 61(2), pp.339–349.

Ferrari, M.C.O. and Chivers, D.P., 2006. Learning threat-sensitive predator avoidance: How do fathead minnows incorporate conflicting information? *Animal Behaviour*,71(1), pp. 19-26.

Ferrari, M.C.O., Ranåker, L., Weinersmith, K.L., Young, M.J., Sih, A. and Conrad, J.L., 2014. Effects of turbidity and an invasive waterweed on predation by introduced largemouth bass. *Environmental Biology of Fishes*,97, pp. 79-90.

Figueiredo, B.R.S., Mormul, R.P., Chapman, B.B., Lolis, L.A., Fiori, L.F. and Benedito, E., 2016. Turbidity amplifies the non-lethal effects of predation and affects the foraging success of characid fish shoals. *Freshwater Biology*,61(3), pp 293-300.

Fischer, S. and Frommen, J.G., 2013. Eutrophication alters social preferences in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*,67, pp. 293-299.

Flock, A. and Wersall, J., 1962. A study of the orientation of the sensory hairs of the receptor cells in the lateral line organ of fish, with special reference to the function of the receptors. *The Journal of cell biology*, 15(1), pp. 19-27.

Franck, D., Dikomey, M. and Schartl, M., 2001. Selection and the maintenance of a colour pattern polymorphism in the green swordtail (*Xiphophorus Helleri*). *Behaviour*, 138(4), pp.467-486.

Fraser, D.F. and Gilliam, J.F., 1987. Feeding under predation hazard: response of the guppy

and Hart's rivulus from sites with contrasting predation hazard. *Behavioral Ecology and Sociobiology*,21, pp. 203-209.

Friard, O. and Gamba, M., 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*,7(11), pp. 1325-1330.

Frost, A.J., Thomson, J.S., Smith, C., Burton, H.C., Davis, B., Watts, P.C. and Sneddon, L.U., 2013. Environmental change alters personality in the rainbow trout, *Oncorhynchus mykiss*. *Animal Behaviour*, 85(6), pp.1199–1207.

Gallardo, B., Clavero, M., Sánchez, M.I. and Vilà, M., 2016. Global ecological impacts of invasive species in aquatic ecosystems. *Global Change Biology*, 22, pp.151–163.

Gauff, R.P.M., Bejarano, S., Madduppa, H.H., Subhan, B., Dugény, E.M.A., Perdana, Y.A. and Ferse, S.C.A., 2018. Influence of predation risk on the sheltering behaviour of the coral-dwelling damselfish, *Pomacentrus moluccensis*. *Environmental Biology of Fishes*,101, pp. 639-651.

Glotzbecker, G.J., Ward, J.L., Walters, D.M. and Blum, M.J., 2015. Turbidity alters pre-mating social interactions between native and invasive stream fishes. *Freshwater Biology*,60(9), pp.1784-1793.

Granqvist, M. and Mattila, J., 2004. The effects of turbidity and light intensity on the consumption of mysids by juvenile perch (*Perca fluviatilis L.*). *Hydrobiologia*, 514(1–3), pp.93–101.

Gray, S.M., McDonnell, L.H., Cinquemani, F.G. and Chapman, L.J., 2012. As clear as mud: Turbidity induces behavioral changes in the African cichlid Pseudocrenilabrus multicolor. *Current Zoology*,58(1), pp. 149-157.

Gray, S.M., Sabbah, S. and Hawryshyn, C.W., 2011. Experimentally increased turbidity causes behavioural shifts in Lake Malawi cichlids. *Ecology of Freshwater Fish*,20(4), pp 529-536.

Gregory, R.S., 1993. Effect of turbidity on the predator avoidance behaviour of juvenile chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences*, 50(2), pp.241–246.

Gregory, R.S. and Levings, C.D., 1996. The effects of turbidity and vegetation on the risk of juvenile salmonids, *Oncorhynchus spp*., to predation by adult cutthroat trout, O. clarkii. *Environmental Biology of Fishes*, 47(3), pp.279–288.

Gregory, R.S. and Northcote, T.G., 1993. Surface, planktonic, and benthic foraging by juvenile chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. *Canadian Journal of Fisheries and Aquatic Sciences*, 50(2), pp.233–240.

Guthrie, D.M. and Muntz, W.R.A., 1986. *Role of Vision in Fish Behaviour. In: Pitcher T.J. (eds) The Behaviour of Teleost Fishes. Behaviour of Teleost Fishes*. Boston, MA: Springer.

Hale, R., Swearer, S.E. and Downes, B.J., 2009. Separating natural responses from experimental artefacts: Habitat selection by a diadromous fish species using odours from conspecifics and natural stream water. *Oecologia*,159, pp.679-687.

Hara, T.J., 1975. *Olfaction in fish*. *Progress in Neurobiology*.

Harcourt, J.L., Ang, T.Z., Sweetman, G., Johnstone, R.A. and Manica, A., 2009. Social Feedback and the Emergence of Leaders and Followers. *Current Biology*,19(3), pp.248-252.

Harrison, X.A., 2014. Using observation-level randomeffects to model overdispersion in count data in ecology and evolution. *PeerJ*, 2(e616), p.DOI 10.7717/peerj.616.

Hartman, E.J. and Abrahams, M. V., 2000. Sensory compensation and the detection of predators: The interaction between chemical and visual information. *Proceedings of the Royal Society B: Biological Sciences*,267(1443), pp. 571–575.

Harvey, B.C. and White, J.L., 2008. Use of Benthic Prey by Salmonids under Turbid Conditions in a Laboratory Stream. *Transactions of the American Fisheries Society*, 137, pp.1756–1763.

Hazelton, P.D. and Grossman, G.D., 2009a. The effects of turbidity and an invasive species on foraging success of rosyside dace (*Clinostomus funduloides*). *Freshwater Biology*, 54, pp.1977–1989.

Hazelton, P.D. and Grossman, G.D., 2009b. Turbidity, velocity and interspecific interactions affect foraging behaviour of rosyside dace (*Clinostomus funduloides*) and yellowfin shiners (*Notropis lutippinis*). *Ecology of Freshwater Fish*, 18, pp.427–436.

Harding H. R., Gordon T. A. C., Wong K., McCormick M. I., Simpson S. D. and Radford A. N., 2020. Condition-dependent responses of fish to motorboats *Biol. Lett,* 16,20200401.

Hecht, T. and van der Lingen, C.D., 1992. Turbidity-induced changes in feeding strategies of fish in estuaries. *South African Journal of Zoology*, 27(3), pp.95–107.

Henley, W.F., Patterson, M.A., Neves, R.J. and Dennis Lemly, A., 2000. Effects of Sedimentation and Turbidity on Lotic Food Webs: A Concise Review for Natural Resource Managers. *Reviews in Fisheries Science*, 8(2), pp. 125-139.

Hess, K.R., 1995. Graphical methods for assessing violations of the proportional hazards assumption in cox regression. *Statistics in Medicine*, 14, pp.1707–1723.

Hiermes, M., Mehlis, M., Rick, I.P. and Bakker, T.C.M., 2015. Habitat-dependent olfactory discrimination in three-spined sticklebacks (*Gasterosteus aculeatus*). *Animal Cognition*,18, pp. 839-846.

Higham, T.E., Stewart, W.J. and Wainwright, P.C., 2015. Turbulence, Temperature, and Turbidity: The Ecomechanics of Predator-Prey Interactions in Fishes. In: *Integrative and Comparative Biology*,55(1), 6-2, pp. 6-20.

Hilton, J. and Phillips, G.L., 1982. The Effect of Boat Activity on Turbidity in a Shallow

Broadland River. *The Journal of Applied Ecology*, 19, pp.143–150.

Hinshaw, J.M., 1985. Effects of Illumination and Prey Contrast on Survival and Growth of Larval Yellow Perch Perca flavescens. *Transactions of the American Fisheries Society*, 114(4), p.1985.

Horkel, J.D. and Pearson, W.D., 1976. Effects of Turbidity on Ventilation Rates and Oxygen Consumption of Green Sunfish, Lepomis cyanellus. *Transactions of the American Fisheries Society*, 105(1), pp. 107-113.

Horppila, J., Liljendahl-Nurminen, A. and Malinen, T., 2004. Effects of clay turbidity and light on the predator-prey interaction between smelts and chaoborids. *Canadian Journal of Fisheries and Aquatic Sciences*, 61(10), pp.1862–1870.

Huenemann, T.W., Dibble, E.D. and Fleming, J.P., 2012. Influence of turbidity on the foraging of largemouth bass. *Transactions of the American Fisheries Society*, 141(1), pp.107–111.

Ioannou, C.C. and Dall, S.R.X., 2016. Individuals that are consistent in risk-taking benefit during collective foraging. *Scientific Reports*, [online] 6(33991). Available at: <https://doi.org/10.1038/srep33991>.

Ioannou, C.C., Payne, M. and Krause, J., 2008. Ecological consequences of the bold-shy continuum: The effect of predator boldness on prey risk. *Oecologia*,157(177).

James, G., Witten, D., Hastie, T. and Tibshirani, R., 2000. *An introduction to Statistical Learning : with applications in R. Current medicinal chemistry*. New York: Springer,19(25), pp.4289-4297.

Janssen, J. and Corcoran, J., 1993. Lateral line stimuli can override vision to determine sunfish strike trajectory. *The Journal of experimental biology*,176, pp.229-305.

Järvenpää, M., Diaz Pauli, B. and Lindström, K., 2019. Water turbidity constrains male mating success in a marine fish. *Behavioral Ecology and Sociobiology*,73, [online] Available at: https://doi.org/10.1007/s00265-019-2752-2.

Järvenpää, M. and Lindström, K., 2004. Water turbidity by algal blooms causes mating system breakdown in a shallow-water fish, the sand goby Pomatoschistus minutus. *Proceedings of the Royal Society B: Biological Sciences*, 271(1555), pp.2361–2365.

Johannesen, A., Dunn, A.M. and Morrell, L.J., 2012. Olfactory cue use by three-spined sticklebacks foraging in turbid water: Prey detection or prey location? *Animal Behaviour*, 84(1), pp.151–158.

Johansen, J.L. and Jones, G.P., 2013. Sediment-induced turbidity impairs foraging performance and prey choice of planktivorous coral reef fishes. *Ecological Applications*, 23(6), pp.1504–17.

Jolles, J.W., Briggs, H.D., Araya-Ajoy, Y.G. and Boogert, N.J., 2019. Personality, plasticity and

predictability in sticklebacks: bold fish are less plastic and more predictable than shy fish. *Animal Behaviour*,154, pp. 193-202.

Kareklas, K., Arnott, G., Elwood, R.W. and Holland, R.A., 2016. Plasticity varies with boldness in a weaklyelectric fish. *Frontiers in Zoology,*13, [online] Available at: https://doi.org/10.1186/s12983-016-0154-0.

Kassambara, A., Kosinski, M. and Biecek, P., 2019. Drawing Survival Curves using 'ggplot2'. R package version 0.4.5. [online] Available at: <https://cran.r-project.org/package=survminer>.

Kemp, P., Sear, D., Collins, A., Naden, P. and Jones, I., 2011. The impacts of fine sediment on riverine fish. *Hydrological Processes*, 25(11), pp.1800–1821.

Kimbell, H.S. and Morrell, L.J., 2015a. 'Selfish herds' of guppies follow complex movement rules, but not when information is limited. *Proceedings of the Royal Society B: Biological Sciences*, 282:(20151558).

Kimbell, H.S. and Morrell, L.J., 2015b. Turbidity influences individual and group level responses to predation in guppies, Poecilia reticulata. *Animal Behaviour*, 103, pp.179–185.

Kimbell, H.S. and Morrell, L.J., 2016. Turbidity weakens selection for assortment in body size in groups. *Behavioral Ecology*, 27(2), pp.545–552.

Krause, J., Ruxton, G., Ruxton, G. and Ruxton, I., 2002. *Living In Groups*. New York: Oxford University Press.

Leahy, S.M., McCormick, M.I., Mitchell, M.D. and Ferrari, M.C.O., 2011. To fear or to feed: The effects of turbidity on perception of risk by a marine fish. *Biology Letters*, 7(6), pp.811–813.

Lehtiniemi, M., Engström-Öst, J. and Viitasalo, M., 2005. Turbidity decreases anti-predator behaviour in pike larvae, *Esox lucius*. *Environmental Biology of Fishes*, 73(1), pp.1–8.

Lewandowski, E. and Boughman, J., 2008. Effects of genetics and light environment on colour expression in threespine sticklebacks. *Biological Journal of the Linnean Society*,94(4), pp. 663-673.

Li, W., Zhang, T., Zhang, C., Li, Z., Liu, J. and Hicks, B.J., 2013. Effects of turbidity and light intensity on foraging success of juvenile mandarin fish Siniperca chuatsi (*Basilewsky*). *Environmental Biology of Fishes*, 96, pp.995–1002.

Lima, S.L. and Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68, pp.619–640.

Linde, A.R., Izquierdo, J.I., Moreira, J.C. and Garcia-Vazquez, E., 2008. Invasive tilapia juveniles are associated with degraded river habitats. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 18(6), pp.891–895.

Lloyd, D.S., 1987. Turbidity as a Water Quality Standard for Salmonid Habitats in Alaska.

North American Journal of Fisheries Management,7(1), pp.34-45.

Lloyd, D.S., Koenings, J.P. and Laperriere, J.D., 1987. Effects of Turbidity in Fresh Waters of Alaska. *North American Journal of Fisheries Management*,7(1), pp. 18-33.

Lunt, J. and Smee, D.L., 2014. Turbidity influences trophic interactions in estuaries. *Limnology and Oceanography*, 59(6), pp. 2002-2012.

Lunt, J. and Smee, D.L., 2015. Turbidity interferes with foraging success of visual but not chemosensory predators. *PeerJ*, [online] e1212. Available at: <https://doi.org/10.7717/peerj.1212>.

Lythgoe, J.N., 1975. The structure and function of iridescent corneas in teleost fishes. *Proceedings of the Royal Society of London - Biological Sciences*, 188, pp. 437–457.

MacDougall, A.S. and Turkington, R., 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology*, 86(1), pp.42–55.

Mainka, S.A. and Howard, G.W., 2010. Climate change and invasive species: Double jeopardy. *Integrative Zoology*, 5(2), pp.102–111.

Martin, C.W., Fodrie, F.J., Heck, K.L. and Mattila, J., 2010. Differential habitat use and antipredator response of juvenile roach (*Rutilus rutilus*) to olfactory and visual cues from multiple predators. *Oecologia*,162(4), pp.893-902.

Martin, D.J., Shelly, A.A., Danehy, R.J., Lang, E.D. and Hvozda, J., 2019. Coho Salmon Growth in Relation to Natural Turbidity Regimes in a Coastal Stream of Northern California. *Transactions of the American Fisheries Society*, 148, pp.817–831.

Martins, C.I.M., Schrama, J.W. and Verreth, J.A.J., 2005. The consistency of individual differences in growth, feed efficiency and feeding behaviour in African catfish *Clarias gariepinus* (Burchell 1822) housed individually. *Aquaculture Research*,36(15), pp. 1509-1516.

Marusov, E.A. and Kasumyan, A.O., 2017. Feeding behavior and responsivity to food odors in Nile tilapia Oreochromis niloticus (Cichlidae) after chronic polisensory deprivation. *Journal of Ichthyology*, 57(5), pp.747–752.

Mazerolle, M.J., 2017. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). *R package version 2.1-1*.

Mazué, G.P.F., Dechaume-Moncharmont, F.X. and Godin, J.G.J., 2015. Boldness-exploration behavioral syndrome: Interfamily variability and repeatability of personality traits in the young of the convict cichlid (*Amatitlania siquia*). *Behavioral Ecology*, 26(3), pp.900–908.

McCormick, M.I. and Manassa, R., 2008. Predation risk assessment by olfactory and visual cues in a coral reef fish. *Coral Reefs*,27, pp.105-113.

McDonald, N.D., Rands, S.A., Hill, F., Elder, C. and Ioannou, C.C., 2016. Consensus and experience trump leadership, suppressing individual personality during social foraging. *Science*

Advances,2(9), [online] Available at: DOI: 10.1126/sciadv.1600892

McMahon, T.E. and Holanov, S.H., 1995. Foraging success of largemouth bass at different light intensities: implications for time and depth of feeding. *Journal of Fish Biology*,46(5), pp. 759 - 767.

Meager, J.J. and Batty, R.S., 2007. Effects of turbidity on the spontaneous and prey-searching activity of juvenile Atlantic cod (*Gadus morhua*). *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1487), pp.2123–2130.

Meager, J.J., Domenici, P., Shingles, A. and Utne-Palm, A.C., 2006. Escape responses in juvenile Atlantic cod Gadus morhua L.: The effects of turbidity and predator speed. *Journal of Experimental Biology*,209, pp. 4174-4184.

Meager, J.J., Solbakken, T., Utne-Palm, A.C. and Oen, T., 2005. Effects of turbidity on the reactive distance, search time, and foraging success of juvenile Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 62(9), pp.1978–1984.

Miner, J.G. and Stein, R.A., 1996. Detection of Predators and Habitat Choice by Small Bluegills: Effects of Turbidity and Alternative Prey. *Transactions of the American Fisheries Society*,125(1), pp.97-103.

Mol, J.H. and Ouboter, P.E., 2004. Downstream Effects of Erosion from Small-Scale Gold Mining on the Instream Habitat and Fish Community of a Small Neotropical Rainforest Stream. *Conservation Biology*, 18(1), pp.201–214.

Ohata, R., Masuda, R., Takahashi, K. and Yamashita, Y., 2014. Moderate turbidity enhances schooling behaviour in fish larvae in coastal waters. *ICES Journal of Marine Science*,71,4, pp.925-929.

Ohata, R., Masuda, R., Ueno, M., Fukunishi, Y. and Yamashita, Y., 2011. Effects of turbidity on survival of larval ayu and red sea bream exposed to predation by jack mackerel and moon jellyfish. *Fisheries Science*,77, pp.207-215.

Ohata, R., Masuda, R. and Yamashita, Y., 2011. Ontogeny of antipredator performance in hatchery-reared Japanese anchovy Engraulis japonicus larvae exposed to visual or tactile predators in relation to turbidity. *Journal of Fish Biology*,79(7), pp. 2007-2018.

Oldham, R.C., Pintor, L.M. and Gray, S.M., 2018. Behavioral differences within and among populations of an African cichlid found in divergent and extreme environments. *Current Zoology*,65(1), pp.33-42.

Pangle, K.L., Malinich, T.D., Bunnell, D.B., DeVries, D.R. and Ludsin, S.A., 2012. Context-dependent planktivory: interacting effects of turbidity and predation risk on adaptive foraging. *Ecosphere*, 3(12), pp.114–118.

Paudel, B., Montagna, P.A. and Adams, L., 2019. The relationship between suspended solids

and nutrients with variable hydrologic flow regimes. *Regional Studies in Marine Science*,25, pp. 104178.

Pekcan-Hekim, Z. and Lappalainen, J., 2006. Effects of clay turbidity and density of pikeperch (*Sander lucioperca*) larvae on predation by perch (*Perca fluviatilis*). *Naturwissenschaften*, 93(7), pp.356–9.

Piyapong, C., Krause, J., Chapman, B.B., Ramnarine, I.W., Louca, V. and Croft, D.P., 2010. Sex matters: A social context to boldness in guppies (*Poecilia reticulata*). *Behavioral Ecology*,21(1), pp. 3-8.

Pohlmann, K., Atema, J. and Breithaupt, T., 2004. The importance of the lateral line in nocturnal predation of piscivorous catfish. *Journal of Experimental Biology*,207, pp. 2971-2978.

Quesenberry, N.J., Allen, P.J. and Cech, J.J., 2007. The influence of turbidity on three-spined stickleback foraging. *Journal of Fish Biology*, 70(3), pp.965–972.

R core Team, 2019. *R: A language and environment for statistical computing.*

Réale, D., Reader, S.M., Sol, D., McDougall, P.T. and Dingemanse, N.J., 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82, pp.291–318.

De Robertis, A., Ryer, C.H., Veloza, A. and Brodeur, R.D., 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 60(12), pp.1517–1526.

Rowe, D.K. and Dean, T.L., 1998. Effects of turbidity on the feeding ability of the juvenile migrant stage of six New Zealand freshwater fish species. *New Zealand Journal of Marine and Freshwater Research*,32(1), pp. 21-29.

Ryan, P.A., 1991. Environmental effects of sediment on new zealand streams: A review. *New Zealand Journal of Marine and Freshwater Research*,25(2), pp. 207-221.

Schwalbe, M.A.B., Bassett, D.K. and Webb, J.F., 2012. Feeding in the dark: Lateral-line-mediated prey detection in the peacock cichlid *Aulonocara stuartgranti*. *Journal of Experimental Biology*,215, pp. 2060-2071.

Sebire, M., Katsiadaki, I., Taylor, N.G.H., Maack, G. and Tyler, C.R., 2011. Short-term exposure to a treated sewage effluent alters reproductive behaviour in the three-spined stickleback (*Gasterosteus aculeatus*). *Aquatic Toxicology*, 105(1-2), pp.78-88.

Seehausen, O. and Van Alphen, J.J.M., 1998. The effect of male coloration on female mate choice in closely related Lake Victoria cichlids (*Haplochromis nyererei complex*). *Behavioral Ecology and Sociobiology*,42, pp. 1-8.

Seehausen, O., Van Alphen, J.J.M. and Witte, F., 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science*,277,(5333), pp. 1808-1811.

Shechonge, A., Ngatunga, B.P., Bradbeer, S.J., Day, J.J., Freer, J.J., Ford, A.G.P., Kihedu, J., Richmond, T., Mzighani, S., Smith, A.M., Sweke, E.A., Tamatamah, R., Tyers, A.M., Turner, G.F. and Genner, M.J., 2019a. Correction to: Widespread colonisation of Tanzanian catchments by introduced Oreochromis tilapia fishes: the legacy from decades of deliberate introduction (Hydrobiologia, (2019), 832, 1, (235-253), 10.1007/s10750-018-3597-9). *Hydrobiologia*, 832(1), pp.235–253.

Shingles, A., McKenzie, D.J., Claireaux, G. and Domenici, P., 2005. Reflex cardioventilatory responses to hypoxia in the flathead gray mullet (*Mugil cephalus*) and their behavioral modulation by perceived threat of predation and water turbidity. In: *Physiological and Biochemical Zoology*,78(5), pp. 744-755.

Shoup, D.E. and Wahl, D.H., 2009. The Effects of Turbidity on Prey Selection by Piscivorous Largemouth Bass. *Transactions of the American Fisheries Society*, 138(5), pp.1018-1027.

Sih, A., Bell, A. and Johnson, J.C., 2004. Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology and Evolution*, 19(7), pp.372–378.

Sih, A., Cote, J., Evans, M., Fogarty, S. and Pruitt, J., 2012. *Ecological implications of behavioural syndromes*. *Ecology Letters*,15(3), pp. 278-289.

Sih, A., Ferrari, M.C.O. and Harris, D.J., 2011. Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, 4(2), pp. 367-387.

van der Sluijs, I., Gray, S.M., Amorim, M.C.P., Barber, I., Candolin, U., Hendry, A.P., Krahe, R., Maan, M.E., Utne-Palm, A.C., Wagner, H.J. and Wong, B.B.M., 2011. Communication in troubled waters: Responses of fish communication systems to changing environments. *Evolutionary Ecology*,25, pp. 623-640.

Sloan Wilson, D., Clark, A. B., Coleman, K. & Dearstyne, T. ,1994. Shyness and boldness in humans and other animals. *Trends Ecol. Evol*. 9,pp. 442–446.

Snickars, M., Sandström, A. and Mattila, J., 2004. Antipredator behaviour of 0+ year *Perca fluviatilis*: Effect of vegetation density and turbidity. *Journal of Fish Biology*, 65, pp.1604–1613.

Snow, R.A., Shoup, D.E. and Porta, M.J., 2018a. Effects of Turbidity on Prey Selection and Foraging Rate of Hatchery-Reared Juvenile Tiger Muskellunge. *North American Journal of Fisheries Management*, 38(2), pp.487–492.

Sohel, S. and Lindström, K., 2015. Algal Turbidity Reduces Risk Assessment Ability of the Three-Spined Stickleback. *Ethology*, 121(6), pp.548–555.

Stamps, J. and Groothuis, T.G.G., 2010. The development of animal personality: Relevance, concepts and perspectives. *Biological Review,* 85(2), pp. 301-325.

Stamps, J.A., 2007. Growth-mortality tradeoffs and 'personality traits' in animals. *Ecology Letters*, 10(5), pp. 355–363.

Stamps, J.A., Briffa, M. and Biro, P.A., 2012. Unpredictable animals: Individual differences in intraindividual variability (IIV). *Animal Behaviour*, 83(6), pp. 1325–1334.

Stuart-Smith, R.D., Stuart-Smith, J.F., White, R.W.G. and Barmuta, L.A., 2007. The effects of turbidity and complex habitats on the feeding of a *galaxiid* fish are clear and simple. *Marine and Freshwater Research*, 58(5), pp.429–435.

Sundin, J., Berglund, A. and Rosenqvist, G., 2010. Turbidity hampers mate choice in a pipefish. *Ethology*,116(8), pp. 713- 721.

Suriyampola, P.S., Cacéres, J. and Martins, E.P., 2018. Effects of short-term turbidity on sensory preference and behaviour of adult fish. *Animal Behaviour*,146, pp.105-111.

Sutherland, A.B. and Meyer, J.L., 2007. Effects of increased suspended sediment on growth rate and gill condition of two southern Appalachian minnows. *Environmental Biology of Fishes*,80, pp. 289-403.

Swanbrow Becker, L.J. and Gabor, C.R., 2012. Effects of Turbidity and Visual vs. Chemical Cues on Anti-Predator Response in the Endangered Fountain Darter (*Etheostoma fonticola*). *Ethology*,118(10), pp.994-1000.

Sweka, J.A. and Hartman, K.J., 2001. Effects of turbidity on prey consumption and growth in brook trout and implications for bioenergetics modeling. *Canadian Journal of Fisheries and Aquatic Sciences*, 58(2), pp.368–393.

Sweka, J.A. and Hartman, K.J., 2003. Reduction of reactive distance and foraging success in smallmouth bass, *Micropterus dolomieu*, exposed to elevated turbidity levels. *Environmental Biology of Fishes*, 67(4), pp.341–347.

Szopa-Comley, A.W., Donald, W.G. and Ioannou, C.C., 2020. Predator personality and prey detection: inter-individual variation in responses to cryptic and conspicuous prey. *Behavioral Ecology and Sociobiology*, 74(70), available at: https://doi.org/10.1007/s00265-020-02854-9.

Therneau, T.M., 2015. A Package for Survival Analysis in S. version 2.38. *Reference Source*.

Tuomainen, U. and Candolin, U., 2011. Behavioural responses to human-induced environmental change. *Biological Reviews*, [online] 86(3), pp.640–657. Available at: <http://doi.wiley.com/10.1111/j.1469-185X.2010.00164.x>.

Turesson, H. and Brönmark, C., 2007. Predator-prey encounter rates in freshwater piscivores: Effects of prey density and water transparency. *Oecologia*, 153(2), pp.281–90.

Tuxbury, S.M. and Salmon, M., 2005. Competitive interactions between artificial lighting and natural cues during seafinding by hatchling marine turtles. *Biological Conservation*,121,(2), pp. 311-316.

Utne-Palm, A.C., 2001. Response of naïve two-spotted gobies *Gobiusculus flavescens* to

visual and chemical stimuli of their natural predator, cod *Gadus morhua*. *Marine Ecology Progress Series*,218, pp. 267-274.

Utne-Palm, A.C., 2002. Visual feeding of fish in a turbid environment: Physical and behavioural aspects. *Marine and Freshwater Behaviour and Physiology*, 35(1–5), pp.111–128.

Utne, A.C.W., 1997. The effect of turbidity and illumination on the reaction distance and search time of the marine planktivore *Gobiusculus flavescens*. *Journal of Fish Biology*,50(5), pp.926-938.

Vitousek, P.M., Walker, L.R., Whiteaker, L.D., Mueller-Dombois, D. and Matson, P.A., 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science*,238(4828), pp. 802-804.

Ward, A.J.W., Thomas, P., Hart, P.J.B. and Krause, J., 2004. Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, 55(6), pp.561–568.

Webster, M.M., Atton, N., Ward, A.J.W. and Hart, P.J.B., 2007. Turbidity and foraging rate in threespine sticklebacks: The importance of visual and chemical prey cues. *Behaviour*, 144(11), pp.1347–1360.

Wellington, C.G., Mayer, C.M., Bossenbroek, J.M. and Stroh, N.A., 2010. Effects of turbidity and prey density on the foraging success of age 0 year yellow perch Perca flavescens. *Journal of Fish Biology*,76(7), pp.1729 - 1741.

Wenger, A.S., Harvey, E., Wilson, S., Rawson, C., Newman, S.J., Clarke, D., Saunders, B.J., Browne, N., Travers, M.J., Mcilwain, J.L., Erftemeijer, P.L.A., Hobbs, J.P.A., Mclean, D., Depczynski, M. and Evans, R.D., 2017. A critical analysis of the direct effects of dredging on fish. *Fish and Fisheries*, 18(5), pp. 967-985.

Wenger, A.S., Johansen, J.L. and Jones, G.P., 2011. Suspended sediment impairs habitat choice and chemosensory discrimination in two coral reef fishes. *Coral Reefs*, 30, pp.879–887.

Werner, E.E. and Anholt, B.R., 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist*,142(2), pp. 242-272.

Wishingrad, V., Musgrove, A.B., Chivers, D.P. and Ferrari, M.C.O., 2015. Risk in a changing world: Environmental cues drive anti-predator behaviour in lake sturgeon (*Acipenser fulvescens*) in the absence of predators. *Behaviour*, 152(2), pp.635–652.

Wong, B.B.M. and Candolin, U., 2015. *Behavioral responses to changing environments*. *Behavioral Ecology*,26(3), pp.665-673.

Wong, M.Y.L., Medina, A., Uppaluri, C., Arnold, S., Seymour, J.R. and Buston, P.M., 2013. Consistent behavioural traits and behavioural syndromes in pairs of the false clown anemonefish

Amphiprion ocellaris. *Journal of Fish Biology*,83(1), pp. 207-213.

Zambrano, L. and Hinojosa, D., 1999. Direct and indirect effects of carp (*Cyprinus carpio L.*) on macrophyte and benthic communities in experimental shallow ponds in central Mexico. *Hydrobiologia*, 408, pp.131–138.

Zengeya, T.A., Robertson, M.P., Booth, A.J. and Chimimba, C.T., 2013. Ecological niche modeling of the invasive potential of Nile tilapia *Oreochromis niloticus* in African river systems: Concerns and implications for the conservation of indigenous congenerics. *Biological Invasions*, 15(7), pp.1507–1521.

Zhang, X., Mei, X. and Gulati, R.D., 2017a. Effects of omnivorous tilapia on water turbidity and primary production dynamics in shallow lakes: implications for ecosystem management. *Reviews in Fish Biology and Fisheries*, 27, pp.245–254.